OYSTERCATCHERS AND COCKLES: A PREDATOR-PREY STUDY

by

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MATHMATICAL SYMBOLS

ABSTRACT

Oystercatchers Haematopus ostralegus and cockles Cerastoderma edule were studied with the aim of understanding the behaviour of predators and the consequences which this behaviour has on the cockle population.

At Traeth Melynog, Anglesey, the cockle density declined down the shore and those at the bottom were larger,older and heavier than those at the top. This pattern was caused by the spat settling at the top of the shore combined with downshore movement of some cockles. As a consequence, both flesh content and size were correlated with prey density.

The profitability (flesh eaten per minute handling time) of cockles increased with their size. According to optimal foraging theory, these larger ones should therefore have been preferred, and this proved to be so.

The rate at which oystercatchers ate cockles followed a type II functional response. The plateau was not caused solely by handling time, nor were satiation or interference important. Analysis of the functional responses of other birds feeding on one prey species showed that in each case the behaviour also conformed with a type II distribution yet neither handling time nor satiation appeared responsible. To account for this, a theoretical model was developed which generates type II functional responses from optimal foraging theory.

Another model was developed which predicts the aggregative numerical response for a given level of interference. Because of correlations between density, size and flesh content within the cockle population at

Traeth Melynog, this model could not be directly applied to the data. But the basic assumption of the model - that oystercatchers obeyed the ideal free distribution - could be tested. It gave a poor fit to the data. There was little measurable interference between oystercatchers feeding on cockles.

The number of oystercatchers on the Ribble fluctuated in parallel with the cockle population. Much of this change appeared to be due to an influx of young birds. This suggests that young birds seek a suitable estuary whilst adults tend to return to the one found whilst young. Thus the change in oystercatcher numbers was an aggregative numerical response rather than a population numerical response.

Due to correlations within the cockle population at Traeth Melynog, profitability reached a maximum value at 25-100 cockles per m^2. Therefore the oystercatchers concentrated their feeding at these relatively low cockle densities. As a result, cockle mortality due to predation by oystercatchers was inversely density dependent over most of the range of densities. However, since cockle movement took place, this pattern of mortality could not be detected in the cockle population.

ACKNOWLEDGEMENTS

I am grateful to my supervisor Professor W.G.Hale for his encouragement and for giving me the opportunities and freedom to make the most of my time as a member of his department.

Mr. E.I.S.Rees and Professor G.E. Fogg generously provided facilities at the Marine Science Laboratories, Menai Bridge during the winters of 1978-79 and 1979-80. Mr. A. Bennett and the Nature Conservany Council allowed me to work at Traeth Melynog.

I was generously given data by Mr. G.Howells on the Birds of Estuaries Enquiry counts for Traeth Melynog; By Dr. P.H.Smith on the oystercatcher numbers on the Ribble; by the South West Lancashire Ringing Group on the age composition of oystercatchers on the Ribble; by Dr. N.B.Davies on the functional response of wagtails and by Dr. J.D.Goss-Custard on the functional response of redshanks.

Dr. Clive Anderson proposed the method of analysing functional responses, found an error in my model of the aggregative numerical response and calculated the equations of the depletion model.

I am indepted to Dr. John Goss-Custard who

encouraged this work and made a considerable number of suggestions and corrections which immeasurably improved this thesis. Dr. Lynn Erselius made many helpful critisisms and drew some of the figures. My father, Alistair Sutherland, made the English more conventional. The Guardian allowed me to use Denis Thorpe's photograph as a frontispiece. Robin Sutton laughed whenever I tried to justify an unconvincing graph.

1. INTRODUCTION

The first theoretical models of the interaction between populations of predators and their prey were developed in the 1920's and 30's (Thompson 1924; Lotka 1925; Volterra 1926; Nicholson 1933 and Nicholson and Bailey 1935). These provided the basis for future studies and refined versions are still used today.

The next major advance came with the classic works of Holling (1959a,b), Watt (1959) and Ivlev (1961). They criticised the major assumptions of the Lotka-Volterra and Nicholson-Bailey models - that the attack rate per predator is a linear function of prey density - and suggested that attack rates rose monotonically towards a maximum as prey density increases. In addition, Watt suggested that searching efficiency may decline as the density of searching predators increases and Ivlev discusses the variations in prey selection with prey density. A further advance was that they derived these ideas from experimental data. Ivlev studied fish and Holling mammals and so showed that, although the complete population changes may be easier to study in insects, other organisms may be better for elucidating how predators actually work.

Further work, especially on arthropods, has confirmed that the major components of predator-prey relationships are 1/ the changes in feeding rate of

individual predators with prey density, 2/ the changes in the number of prey with prey density and 3/ the degree of interference between predators (Hassell 1978). The change in feeding rate with prey density has been termed the functional response, and the changes in the number of predators has been termed the numerical response (Solomon 1949).

Studies on predator-prey relationships have frequently been of parasitoids, which often have a single host only, and this host is unlikely to vary markedly in size. Consequently, such studies have been able to ignore factors influencing prey selection. Many predators will encounter prey of different species and different sizes (usually of different ages), and will have to decide which to eat. The decision of which prey types to eat is likely to be influenced by prey density. This could have important consequences for the functional and numerical responses of the predator and for the population dynamics of the prey. The importance of predators switching between prey types has been considered (Murdock and Oaten 1975) but the other consequences of prey selection e.g. taking fewer species or size classes at higher prey densities have largely been ignored.

There has recently been a trend towards developing a general theory of foraging behaviour which describes the choices made for prey type and place in which to feed.

Following the initiative of MacArthur's optimisation models e.g. MacArthur and Pianka (1966), there has been a succession of theoretical models describing the optimal behaviour of foraging predators. Collectively known as optimal foraging theory, this has proved fairly successful in predicting the behaviour of predators (Pyke et al 1977; Krebs 1978). This provides an opportunity to understand the predator responses that underly the major components of the predator-prey relationship in terms of a general theory of prey and place selection. I shall therefore attempt to link optimal foraging theory with population dynamics in this study.

Previous to this study, studies of predator-prey systems and tests of optimal foraging theory have been done separately. Investigations into predator-prey relationships have normally involved arthropods whilst most tests of optimal foraging theory have used vertebrates. Oystercatchers and cockles provide an excellent opportunity to combine these two approaches. Individual oystercatchers specialise on one prey type (i.e. they can be considered monophagous), the populations of both predator and prey are easy to count and their environment is simple and two dimensional. The foraging behaviour of oystercatchers is easy to quantify and the predated shells are left on the surface so that prey size is easily determined. Oystercatchers and cockles may thus be used to gain insight into the foraging behaviour of predators and so

understand the mechanisms underlying predator-prey systems.

The major aims of this thesis are thus to (1) describe the responses of the oystercatcher to the cockle population i.e. the size selection, functional response and aggregative numerical response (2) test whether optimal foraging theory can explain these responses (3) examine the consequences of these responses for the pattern of mortality inflicted on the cockle population.

THE STUDY AREA

Most ecological research is based upon studying the responses of organisms to variations in their environment. For predator-prey studies it is essential to have variations in the prey population. It was therefore important to have a site in which the cockles varied in age, size and density.

The original intention was to study the oystercatchers and cockles on the Ribble Estuary, Lancashire. During my first year I discovered that all the cockles present were from the 1975 spatfall and thus were of uniform age and size. I therefore decided to find a more suitable site and in September 1978 moved to Traeth Melynog, Anglesey.

In some parts of Traeth Melynog the cockle population exceeded 600 cockles per m^2 and included a wide range of ages and sizes. As the substrate was sandy the conditions were excellent for observing the oystercatchers and sieving the cockles. The bay was buffered from the severest weather of the 1978/79 cold winter by the proximity of the Gulf Stream so that both the cockles and I survived. During the study period there was no cockle fishing and very little disturbance from people.

Traeth Melynog is a sheltered east facing, sandy bay about two kilometers wide adjoining Newborough Warren on the southern tip of Anglesey. It is roughly rectangular

and has an intertidal area of about 330 hectares not including the adjacent but seperate sand banks in the strait (Fig. 1.1). The inner margin is fringed by a very narrow saltmarsh in front of the dunes. The upper shore becomes stony east of the Briant. At low water the flats end in a complex of channels and steep sided sand banks. Details of the tidal pattern and the invertebrate populations are given in Rees and Walker (1976).

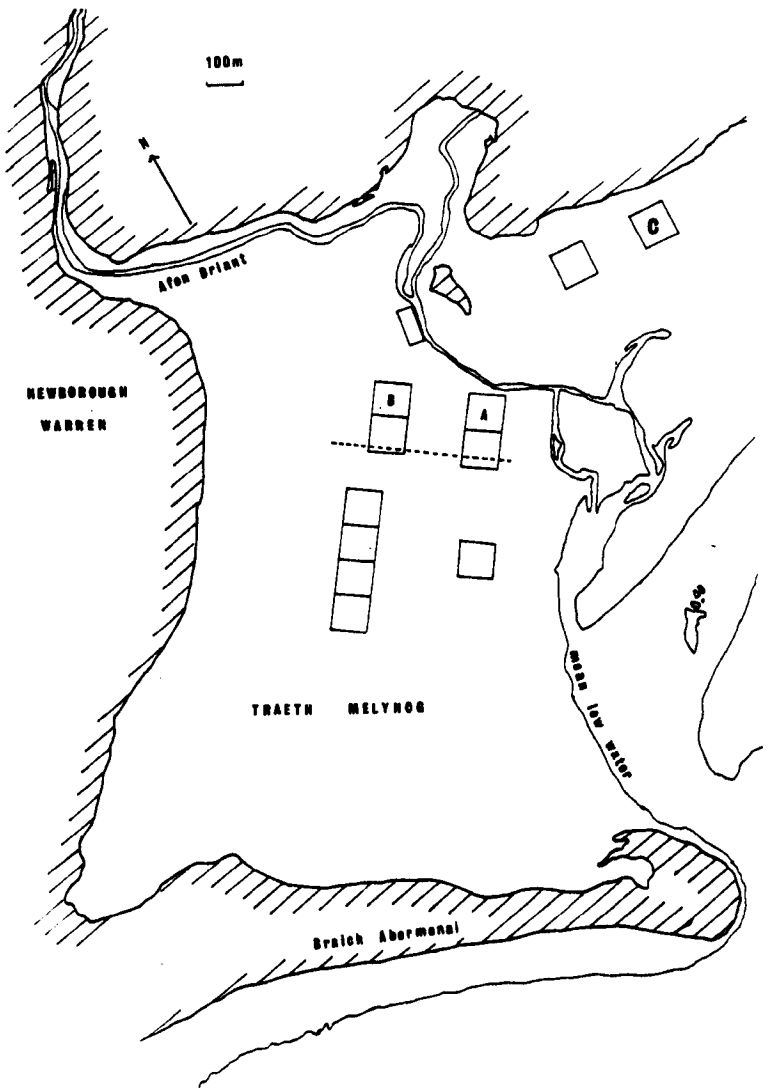


Fig. 1.1 Traeth Melynog, the positions of the observation sites ☐ and the transect (----). Letters refer to sites mentioned in text.

2. THE ROLE OF PARASITES AND OTHER PREDATORS

Oystercatchers eat second winter and older cockles, so the main aim of this study was to determine the effect of oystercatchers on the populations of the older cockles. Oystercatchers, however, are not the only biotic source of mortality to the cockle, and so the possible roles of other predators (birds, fish, crabs and man) and parasites must also be assessed.

a/ Birds

Table 2.1 shows the results of the Birds of Estuary Enquiry counts for Traeth Melynog. The counts for 1979-80 were taken from one part of the sand dunes from which not all of the bay was visible and may be an underestimate of the total numbers present.

The most likely important predator of cockles is the knot (*Cal dris canutus*) which often feeds on cockles (Davidson 1971; Goss-Custard *et al* 1977a). However Goss-Custard et al (1977a) found that although cockles can be a major part of the diet of knot they seldom ate cockles over 10mm in length, probably because they lack the large beak and gape necessary to tackle such difficult prey. If knot regularly took large cockles at Traeth Melynog it would certainly have been noticed.

Other birds have been reported eating cockles

SPECIES		Sep	Oct	Nov	Dec	Jan	Feb	Mar
Shelduck Tadorna tadorna	79-80	8		10	30	56	74	64
Mallard Anas platyrhynchos	79-80	124	14	6	9			
Teal Anas crecca	79-80	3		49		5		
Wigeon Anas penelope	79-80	3	282	884	330	c2000	62	
Pintail Anas acuta	79-80	2	12	21	8	21	16	
Shoveler Anas clypeata	79-80		1	2				
Red-breasted Merganser Mergus serrator	79-80		7	2			3	12
Oystercatcher Haematopus ostralegus	69-75	190	254	275	340	389	310	49
	79-80	350	350	300	250	300	150	209
Ringed plover Charadrius hiaticula	69-75		65	102	77	40	83	23
	79-80		2					
Grey plover Pluvialis squatarola	69-75		31	85	21	44	55	
	79-80		2	2	2		38	10
Lapwing Vanellus vanellus	69-75	6	7	650	1100	320	675	15
	79-80							
Turnstone Arenaria interpres	69-75		180	20	6	29	113	44
	79-80							
Knot Calidris canutus	69-75		34	38	5	7	10	3
	79-80	1						
Dunlin Calidris alpina	69-75		310	465	670	750	585	32
	79-80	5	35	26	12	100	230	3
Redshank Tringa totanus	69-75	34	101	260	95	135	120	6
	79-80	14	95	75	67	70	130	173
Greenshank Tringa nebularia	69-75	7	4	1	2	1	1	
	79-80	1	4	3		1		
Bar-tailed Godwit Limosa lapponica	69-75	1	9	39	66	90	104	2
	79-80	1	9			28		
Curlew Numenius arquata	69-75	32	28	170	330	40	200	10
	79-80	89	263	12	42	180	298	55

Table 2.1 Birds of Estuaries Enquiry counts for Traeth Melynog for 1979-80 and mean wader counts for 1969-75. Data provided by Mr. G. Howells.

elsewhere: herring gulls Larus argentatus on the Waddensee (Kreger 1940), redshank Tringa totanus, dunlin Calidris alpina, and turnstone Arenaria interpres on Morecambe Bay and the Wash (Davidson 1971; Jones 1975). At Traeth Melynog, herring gulls only ate cockles stolen from oystercatchers. Redshank, dunlin and turnstone were never seen scavenging large damaged cockles (as observed on the Wash) although they may have eaten spat cockles. No other birds were present whose diet is known regularly to include cockles (Witherby 1941; Davidson 1971), nor were any other birds ever seen eating large cockles (which would be conspicuous). Apart from the oystercatcher, the contribution of birds to the mortality of older cockles is almost certainly negligible.

b/ Fish

Fishermen using stake nets or a long line positioned alongside the river at Traeth Melynog stated that they caught flounders Pleuronectes flesus, and occasionally plaice Pleuronectes platessa, but no other bottom feeding fish.

Flounder are reported as eating Crustacea, Annelids and Molluscs - the proportion of each prey species varying between sites, ages of fish and even years (Herdman and Scott 1895; Ascroft 1900; Murie 1903; Blegvad 1932; Larsen 1936; Hartley 1940; Williams, Perkins and Hinde 1963; Hancock and Urquhart 1965). In

many of these studies cockles were an important part of the diet.

Flounders on Llanrhidian Sands (South Wales) ate, on average, 120 brood cockles per high water period in the three months August to October. Gut analysis showed that large cockles were only taken when small ones were scarce, and then only in small numbers (Hancock and Urquhart 1965).

The consumption of estuarine invertebrates by flounders is likely to be greatly reduced in the winter. Hartley (1940) found that on the Tamar and Lyner estuaries the immature flounders fast during the winter. Mature fish begin to fast later although most of the pre-spawning fish left in January. Furthermore Williams et al. (1963) found that flounders move offshore in the winter. Although it is possible that flounders are an important predator of spat cockles in the summer, the predation of older cockles by flounders in winter is likely to be negligible.

c/ Crabs

Shore crabs Carcinus maenas may predate heavily on cockles but only the larger ones are likely to attack the older cockles. Orton (1926) concluded that the shore crab was a major predator of small cockles. B.W.Jones (in Hancock and Urquhart 1965) showed that crabs 50-70mm

wide ate up to 39 first winter cockles (c15mm) per day. There was a tendency for the smallest in the range 10-22mm to be eaten first. Elner and Hughes (1978) showed that the size of mussels Mytilus edulis taken by shore crabs depended upon the crab size, and that large crabs are capable of taking ones 60mm long and probably eat large cockles too.

It seems that large crabs severely reduce their feeding in intertidal areas in midwinter. Naylor (1962) showed that crabs larger than 35mm carapace width migrated up the shore on each high tide and back again with the ebb, but in summer many were left stranded below stones at low tide. In December and March they still migrated upshore but few were left stranded while in January and February upshore migration ceased. On the Ribble and at Traeth Melynog the fishermen asserted that there were few crabs active in the winter but that in the summer crabs were common and often removed bait from their lines. No crabs over 15mm carapace width were found during the sampling in the winter at Traeth Melynog (see Chapter 3 for details of sampling programme). B.W.Jones (in Hancock and Urquhart 1965) found that below 6°C adult crabs virtually stopped feeding - although crabs have been caught in baited pots at temperatures of 4°C (Hancock and Urquhart 1965). Thus although crabs eat cockles and are capable of tackling large bivalves, during the winter they tend to stay offshore and feed less, which suggests

they are unlikely to be important predators of large cockles during the winter.

d/ People

On only three occasions during the winters of 1978/79 and 1979/80 did I see people collecting cockles and in each case they removed less than a bucketfull. I was, without a doubt, the major cockle fisherman during these winters and I removed only a negligible proportion (less than 0.1% from each observation site).

e/ Parasites

Cockles are hosts to a wide range of parasites (Cole 1956) of which two Trematodes can be important to the population dynamics of cockles. Cercaria bucephalopsis haimeana (Lacaze-Duthiers 1854) causes castration and was recorded in 12% of Burry Inlet cockles (Hancock and Urquhart 1965). Meiogymnophallus minutus (Cobbold 1859) was found under the hinge of all cockles older than one year examined in the Burry Inlet (Bowers and James 1967). Pistoor (1969) found that this parasite can cause heavy losses of young cockles on the Dutch cockle beds during the summer.

No data were collected on the parasites on the cockles of Traeth Melynog. Old cockles were often seen lying on the surface with the valves apart and may have been dying from an overburden of parasites. Whether

either of these two trematodes kills older cockles is not known but their effect could worsen at times of stress, such as cold winters. They could also render cockles more susceptible to being eaten by oystercatchers, as does the trematode Parorchis acanthus with dogwhelks Nucella lapillus (Feare 1971).

f/ Conclusions

Birds, fish,crabs and man are all potential predators of cockles. It is probable that the fish and crab species present at Traeth Melynog fed very little over the winter and rarely took old cockles. Apart from the oystercatchers, no bird regularly fed on second winter or older cockles. There was practically no cockle fishing. Trematode parasites were probably widespread but their effect on winter mortality is not known. Predators other than the oystercatcher, thus appear to make a negligible contribution to winter mortality of cockles over one year old.

3. THE COCKLE POPULATION

INTRODUCTION

Theoretical predator-prey models usually assume that the composition of the prey is constant at all prey densities i.e. that age structure, sex ratio, growth rate, calorific value, behaviour do not vary with density. This is helpful for producing general, though simplified models, but such factors may be of crucial importance when relationships are studied in detail. In this study, it quickly became apparent that there were trends in age and size in the cockle population down the beach and that these could confound any analysis involving cockle density. It was therefore necessary to describe these in order to understand their effect on any responses the birds might show to cockle density. Indeed it is quite possible that such factors completely override any influence of prey density, and are of prime importance in determining where, and at what rate, oystercatchers feed. I therefore laid out a transect down the beach to look for trends in these parameters: age, size, growth rate, flesh content and density.

In August 1979, samples were taken from eight points at 70m intervals along a transect down the beach (Fig. 1.1). At each point, ten samples were taken at random from within a circle ten meters in diameter. For each sample, a 1/10 m^2 core was inserted into the mud and the top 10cm dug out - no cockles were ever found beneath five centimeters. The sample was washed through a sieve of 7 x 7mm mesh which let spat cockles through but saved time. A visual estimate of the abundance of spat was made at each site.

Back in the lab, the length (anterior to posterior margins) of each cockle was measured to the nearest 0.1mm. Each cockle was aged according to the number of rings on the shell formed if a cockle experiences other shocks e.g. being washed out of the substrate (Orton 1926). They are, however, generally less pronounced than winter rings and usually do not completely encircle the shell, tending to fade away at the margins (Cole 1956). Winter rings form a fairly consistent pattern with the amount of shell produced between winters, declining as the cockles aged (Cole 1956; Boyden 1972). Those rings which I considered to be disturbance rings usually violated this pattern, and this provided confidence in my ability to separate winter rings from disturbance rings.

Another difficulty is that wear in the umbro regions may obliterate the ring laid down in the first winter (Fraser 1932; Boyden 1972). It can then be difficult to distinguish the first winter ring of a fast growing cockle from the second winter ring of a slow growing one. This problem foils attempts to age many species of bivalve (Soemodihardjo 1974; Taylor and Venn 1978). Spat cockles at Traeth Melynog are so small (c5mm long) - presumably due to late spatfall or slow growth - that any ring produced in the first winter cannot be mistaken for a ring produced by a second winter cockle (which would be 10-20cm long). Any abrasion in the umbro region will thus not hinder ageing.

Ash free dry weights were determined by taking ten 29-30mm long cockles from each site along the transect - except where none were of this size. They were then extracted from their shells (this was made easier by freezing them first), left at 90°C for 24 hours in a crucible, and then weighed to obtained dry weight. They were then placed in a muffle furnace at 550°C for two hours, allowed to cool to room temperature in a desiccator, and then reweighed. The difference between the two weights was the ash free dry weight (AFDW). This can be converted into joules by multiplying by 21.65 (Hulscher 1974).

The cockles were sampled from each observation site

(Fig. 1.1) in the middle of each two month observation period (Nov-Dec; Jan-Feb; Mar-Apr) in the winter of 1978-79. Ten random 1/10 m^2 replicates were taken from each site, except those with low cockle densities (below 100 cockles per m^2) when twenty replicates were taken. All the cockles collected were aged and their length measured. Forty cockles, of as wide a size class as possible, were taken from each sample, their length was measured and their AFDW determined. The regression of Log AFDW against Log length was computed. Log values were used for the regression as this produced a more linear relationship. The AFDW of any length cockle could then be assessed for each sample.

An additional set of forty samples was taken from site A (see Figure 1.1) in July 1980 to see if the age structure of the cockle population there had changed during the two years of the study.

(1) Age and length

The height on the beach influenced age distribution (Fig. 3.1). At the top of the transect young cockles predominated and visual estimates showed that spat cockles were restricted to the top four sites. At the bottom of the shore the majority of the cockles were four years old or more. All sampling within the observation sites confirmed this pattern of age distribution. The mean length of each age of cockle increased down the beach (Fig. 3.2). Figure 3.3 shows the age structure of the cockle population in observation site A in September 1978 and July 1980. There are insufficient 1-3 year old cockles in 1978 to account for the numbers of 3-5 year olds two years later. This suggests that there has been immigration of younger cockles to this site.

These trends in age distribution and growth rate result in mean size increasing down the shore (Fig. 3.4). At the top of the shore the cockles are young and slow growing: at the bottom they are older and fast growing. Over the part of the transect on which the oystercatchers feed (all except the top two sites and the bottom one), the mean length of cockles is inversely related to cockle density. The cockles from the observation sites confirmed this pattern. They were divided into size

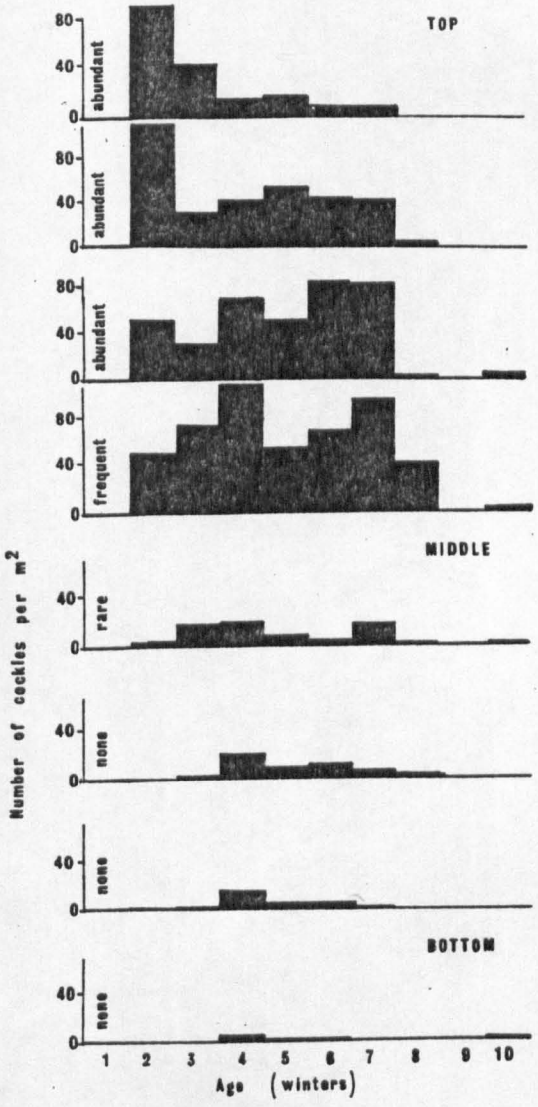


Fig. 3.1 The age distribution of cockles at 70m intervals down a transect down the beach in August 1979.

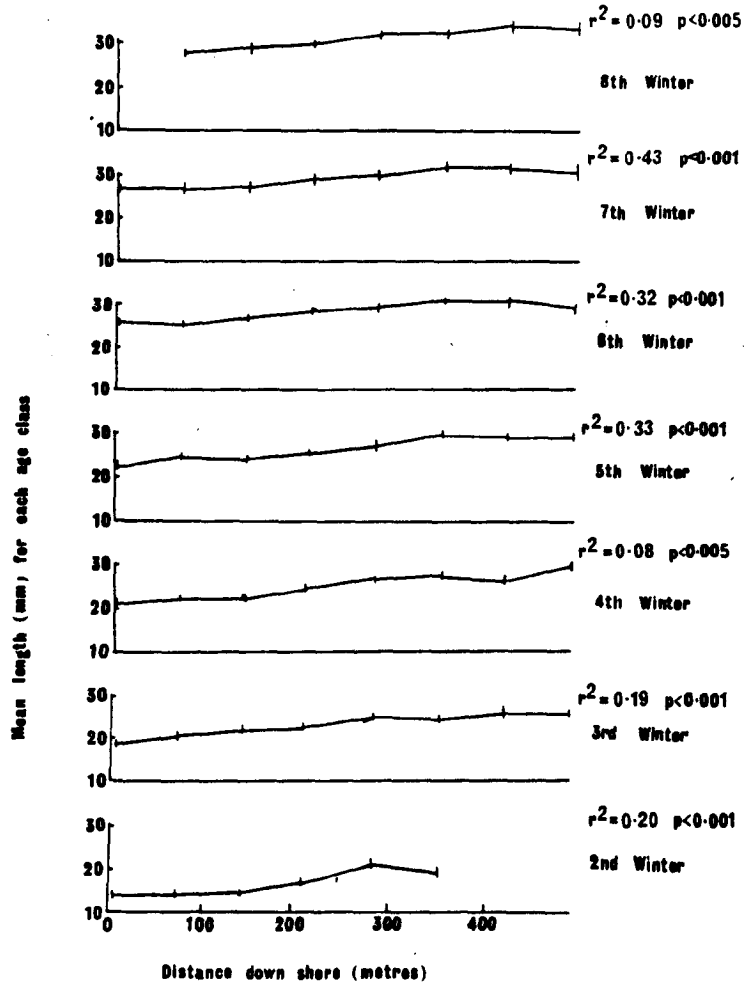


Fig. 3.2 The mean size of each age class of cockle at different heights on the beach.

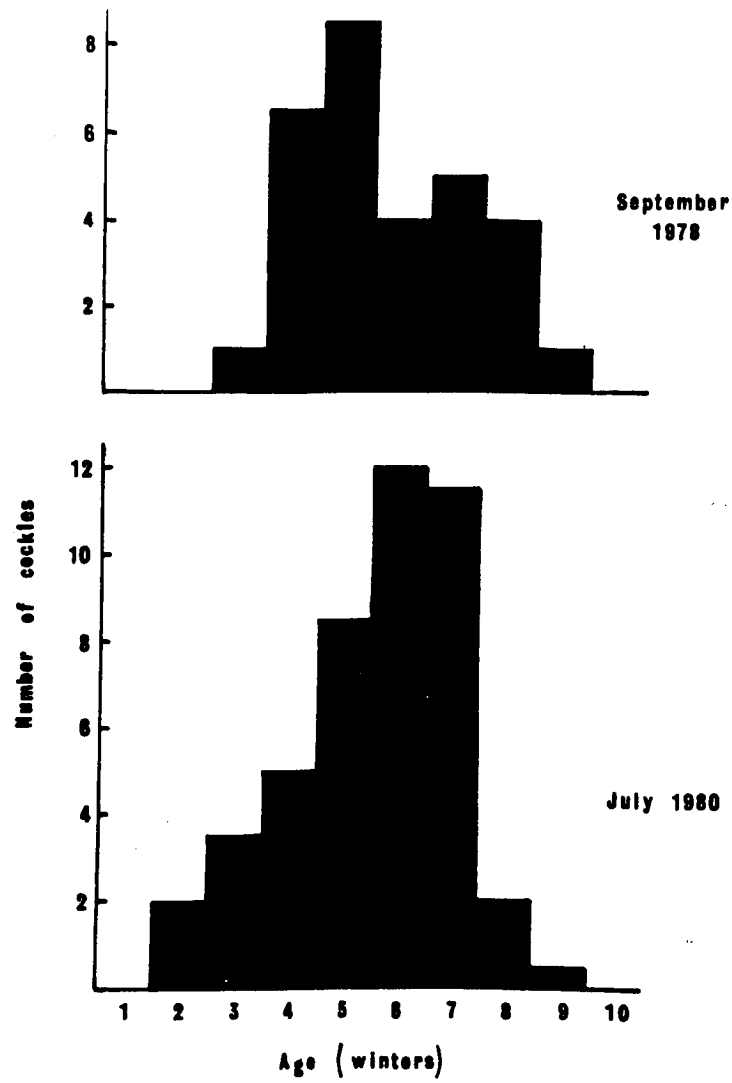


Fig. 3.3 The age distribution of cockles in site A in September 1978 and July 1980.

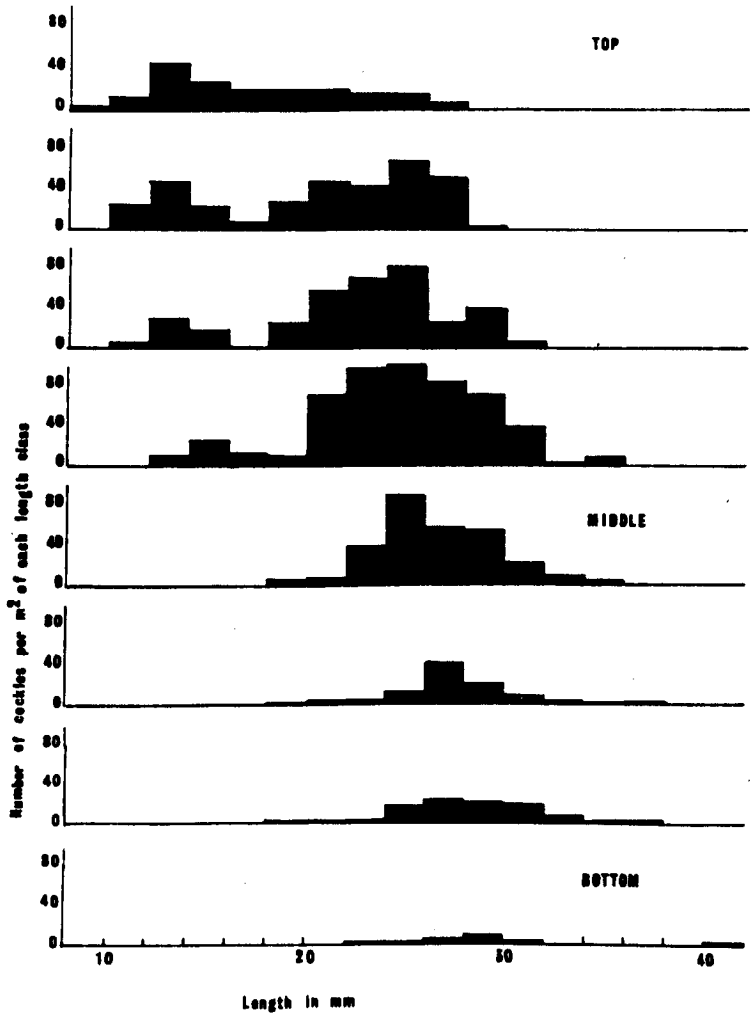


Fig. 3.4. The size distribution of cockles along a transect down the shore at 70m intervals.

classes to analyse size selection (Chapter 4) and the proportion of the smaller cockles increased with cockle density (Fig. 3.5).

(2) Flesh content

The energy content of 29-30mm long cockles was two to three times greater at the bottom of the shore than at the top (Fig. 3.6). In the areas where the oystercatchers feed, the cockle population also declines down the shore so the energy content for a given sized cockle will be inversely correlated with cockle density. This is shown by the analysis of data from the observation sites (Fig. 3.7).

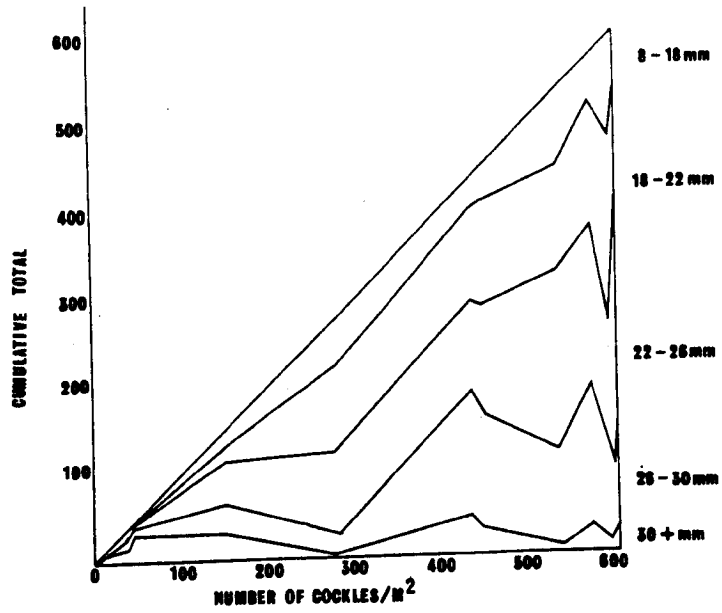


Fig. 3.5 The size composition of cockles at each of the observation sites

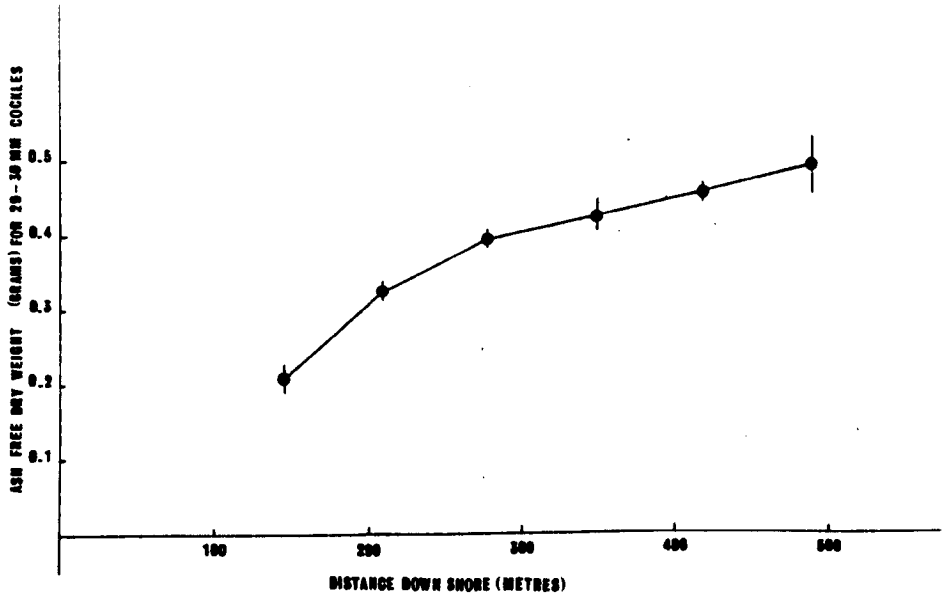


Fig. 3.6 The ash free dry weight of 29-30mm cockles at different sites down the shore.

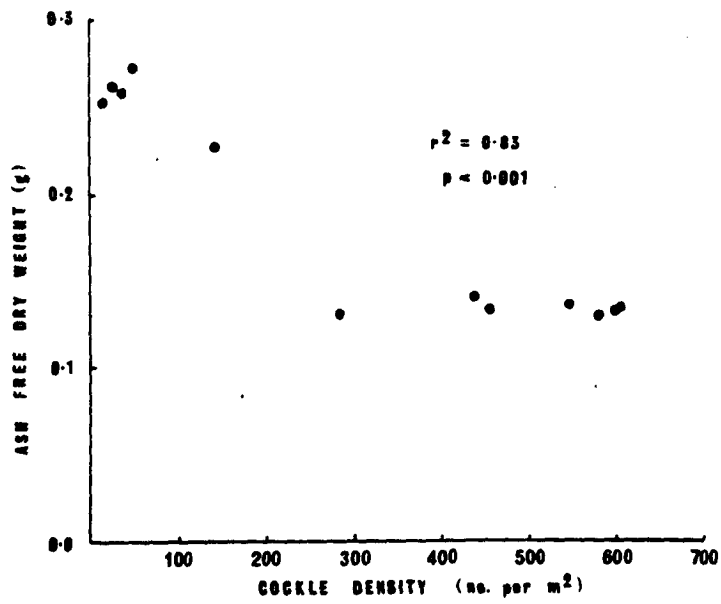


Fig. 3.7 The ash free dry weight of 28.0 mm cockles in January/February in relation to cockle density.

DISCUSSION

(a) Growth rate

The sizes of cockles of each age at Traeth Melynog are compared in Table 3.1 with published values from other sites. The cockles grew slower on my study areas than elsewhere. Two factors make me confident that this slow growth rate was not an artefact produced by misaging cockles. Spat at Traeth Melynog reach only about 5mm in their first winter. This is much smaller than in other studies yet their age is indisputable. Moreover near the top of the shore in August the distribution of cockle lengths is bimodal (see Fig. 3.4). The peak of small cockles are not spat, as very young spat were present (but passed through the sieve) so they must be second winter cockles - which is how they were aged according to their winter rings. These second winter cockles are much smaller than in other studies (Table 3.1).

In previous studies of oystercatchers predating cockles the second winter cockles have been preferentially taken (Drinnan 1957; Hancock and Urquhart 1965; Davidson 1967), but second winter cockles were taken in proportion to their abundance at Greyabbey Bay (Ireland) where cockles were much smaller than in other studies (Brown and O'Connor 1974). As the cockles grew more slowly at Traeth Melynog than elsewhere it is likely that the oystercatchers will not select the second winter cockles.

LOCATION OF POPULATION	0-1year	1-2year	2-3year	3-4year	4-5year	AUTHORITY
River Yealm, Plymouth	19-22	28-31	36-37	35-39	41-45	Orton (1926)
Swansea Bay, S.Wales	17.4	24.0	-	-	-	Wright (1926)
Maplin Sands, Essex	11.1	-	22.0	28.0	-	Wright (1926)
Lancashire coast	13-15	21-34	21-38	29-40	-	McCloy et al (1937)
Waddensee	19-22	28-32	33-36	35-39	-	Kreger (1940)
Waddensee littoral flat	19.5	28.1	32.0	-	-	Kristenson (1956)
Waddensee in creek	14.0	20.6	25.6	-	-	Kristenson (1956)
Range of sites U.K.	9-16	18-28	23-33	31-40	32-42	Cole (1956)
Llanrhidian sands, Wales	13	21-24	26-27	28-29	30	Hancock (1965)
Crouch Estuary, S.Wales	16.8	27.5	31.7	33.9	35.8	Boyden (1972)
Traeth Melynog top		13.3	18.9	20.5	22.4	This study
Traeth Melynog bottom		16.0	24.2	27.2	28.9	This study

Table 3.1 Variation in length (mm) of cockles of different ages from different localities

(b) Age structure

Most other studies have shown considerable mortality of cockles in their second winter and each subsequent winter so that cockles over five years old are scarce (Kreger 1940; Hancock and Urquhart 1965; Brown and O'Connor 1974). At Traeth Melynog the mortality was far less severe as cockles in their seventh winter were frequently encountered.

(c) Trends down the shore

There were insufficient spat and young cockles at the sites at the bottom of the shore to maintain the population of older cockles present (Figs. 3.1 & 3.3). This suggests that either cockles arrive as spat at the top of the beach and move down in subsequent years or the site of spatfall has been gradually moving up the beach each year.

The best way of determining whether the observed distribution of age classes is due to downshore movement is to follow the population for a number of years; if the population of old cockles at the bottom of the beach is maintained and there are never any young cockles present there, then these old cockles must have moved down the beach. If the recorded distribution of age classes is due to changes in the site of spatfall then either the position of subsequent spatfalls must change or cockles at the bottom of the beach must go

extinct. There were insufficient 1-3 year olds at the bottom of the beach in 1978 to account for the numbers of 3-5 year olds there two years later (Fig. 3.3). Thus downshore movement appears to be responsible for the observed distribution of size classes.

Cockle movement has also been suggested to occur at Southport where there appear to have been large scale changes in the distribution of the cockles between 1976 and 1979 (Lancashire and Western Sea Fisheries Scientific Reports for 1976 and 1978). Is this movement active or passive? Active movement is unlikely to be important. Of twenty cockles kept in an aquarium for two months, all but one stayed within five cm of the site in which it was placed. The exceptional individual moved 65cm in one night and 15cm the following night. Similarly Orton (1926) using a completely enclosed box in the field found that almost all the cockles remained in the half of the box in which he had placed them. In some sites in the Waddensee the tracks of actively moving cockles can be seen but these rarely exceed half a meter in length (Kreger 1940).

Some downshore movement definetely occurs at Traeth Melynog as cockles can be watched rolling downshore along the water's edge. This is particularly common when spring tides and gales occur together. As further evidence of movement under these conditions many

cockles are stranded along the edges of channels. Downshore movement has been recorded in Macoma balthica on the Wash by Reading (1979) who also concluded that the movement was passive.

(d) Implications for predator-prey studies

Whatever the reason for these trends, they may be important in determining the pattern of mortality inflicted by the oystercatchers. Many of the important concepts of population dynamics such as density dependence, functional responses and optimal foraging theory assume that prey composition does not vary with prey density. In the part of Traeth Melynog where oystercatchers feed, both mean cockle size and flesh content of a given sized cockle were inversely correlated with density. These relationships are likely to affect the oystercatcher's behaviour and may confound attempts to understand the underlying processess.

SUMMARY

Cockles grew more slowly at Traeth Melynog than in other studies and were longer lived than in many studies.

Spat settle at the top of the beach so cockles are abundant there. The cockles at the bottom of the beach were all old and had been washed down the shore. At the top of the beach cockles are abundant, young and slow growing; at the bottom they are scarce, old and fast growing. Thus mean size increases down the shore and is inversely correlated with cockle density. The flesh content for a given sized cockle increased down the beach and so is inversely correlated with cockle density.

4. PREY SIZE SELECTION

INTRODUCTION

Predators are normally faced with an array of potential prey. They then have to decide which species to eat, what size classes they should eat and how fast they should eat. Theoretical solutions to these problems have been developed by assuming that, as a result of evolutionary selection pressures, animals will tend to harvest their food effectively. If we know how effectiveness is defined by natural selection, it is possible to predict how a predator should behave. Most foraging models and their tests assume that predators aim to maximise their net rate of food intake whilst foraging. Other 'goals' such as maximising the intake of protein (or any other nutrient), minimising the amount of time during which no food can be found or obtaining a balanced diet are possible.

Oystercatchers and bivalves provide an excellent opportunity for studying the factors affecting size selection. The cockles present in the mud can be easily sampled, measured and aged. The shells of predated cockles can be collected from the surface of the mud. Although oystercatchers feed on a wide range of food items, individual oystercatchers in winter usually specialise on only one prey type (see Chapter 5). For

this analysis it is possible to ignore all other prey types as they are ignored by the oystercatchers specialising in cockles. All cockles are likely to contain approximately the same nutrient composition; if oystercatchers maximise the intake of protein, for example, they will inevitably maximise the energy intake. Thus, although the results are always expressed in terms of energy, it is accepted that this is not necessarily the only consideration.

Theoretical considerations

The energy (E) gained from eating a prey item, and its handling time (Th), determine its value (E/Th). If a searching predator encounters two prey types (type 1 of greater value than type 2) at rates λ_1 and λ_2, then specialisation on type 1 will be favoured over specialisation on both types when the rate of energy intake from the former exceeds that from the later i.e. when

$$\frac{\lambda_1 Th_1}{1 + \lambda_1 Th_1} > \frac{\lambda_1 E_1 + \lambda_2 E_2}{1 + \lambda_1 Th_1 + \lambda_2 Th_2}$$

(Charnov 1976). In Figure 4.1, A shows the combination of conditions under which specialisation should occur. This model shows that

(1) The prey with the highest E/Th value should be preferred.

(2) The predator should either take just the most

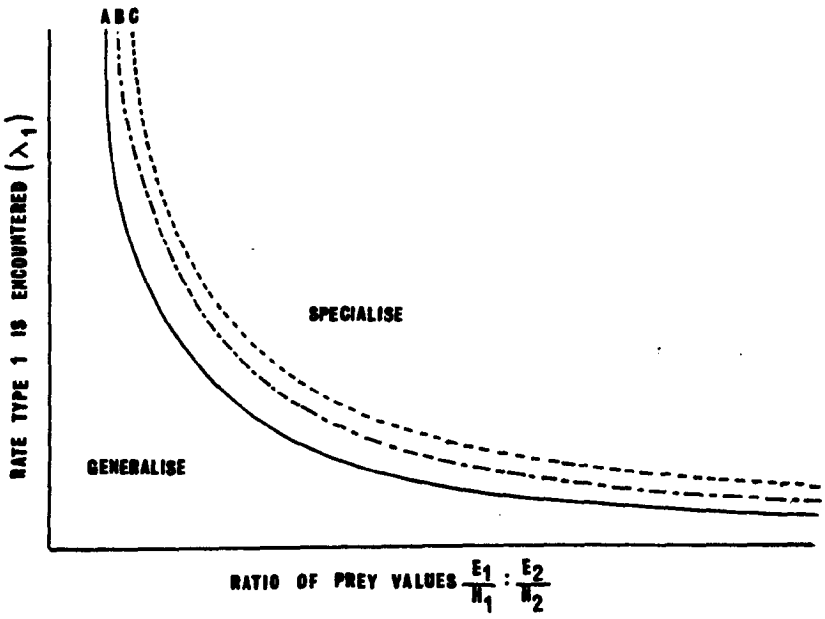


Fig. 4.1 Combination of values of encounter rate on prey type 1 and ratio of prey values under which predators should specialise or generalise.

A = no misidentification

B = misidentification but encounter rate unaffected.

C = misidentification and encounter rate affected.

profitable prey or it should take both types. There are no conditions under which it should specialise on the less profitable prey, even if that prey is exceedingly abundant.

(3) For a given ratio of prey profitabilities, whether or not it takes the less profitable prey depends entirely upon the encounter rate of the less profitable prey.

This model, like practically all foraging models, assumes that the predator has perfect knowledge of the prey. Recognition stimuli must be used to classify prey: crabs apparently use some function of shell size to estimate shell content (Elner and Hughes 1978), and Goss-Custard (in press a) suggests that redshank Tringa totanus use burrow size and surface disturbance to estimate worm size. The cognitative limitations of predators may prevent perfect assessment of prey value from the available recognition stimuli, allowing the possibility of misidentification to occur. What effect is misidentification of prey value likely to have on a predator's choice?

If the same proportion θ of each prey type is mistaken for the other then the number of less profitable prey in the specialised diet is $\theta\lambda_2$, the energy gained from these is $\theta\lambda_2 E_2$, and the increase in handling time is $\theta\lambda_2 Th_2$. Similarly, $\theta\lambda_1$, type 1

prey are excluded from the specialised diet and $(1-\theta)\lambda_1$ included. In the specialised diet the energy gained from type 1 prey is thus $(1-\theta)\lambda_1 E_1$ and the handling time is $(1-\theta)\lambda_1 Th_1$. It then pays to specialise when

$$\frac{(1-\theta)\lambda_1 E_1 + \theta\lambda_2 E_2}{1 + (1-\theta)\lambda_1 Th_1 + \theta\lambda_2 Th_2} > \frac{\lambda_1 E_1 + \lambda_2 E_2}{1 + \lambda_1 Th_1 + \lambda_2 Th_2}$$

As misidentification increases, the specialised diet consists of more inferior type 2 prey and fewer type 1. This will reduce the apparent difference between the values of the two prey types and favour generalisation (see B in Fig. 4.1).

This model assumes that the encounter rate will not be affected - which will be the case if the same number of each prey is mistaken for the other. If different numbers of each prey are mistaken, it will appear to the predator that the encounter rate is also affected. If the more valuable prey is mistaken for the less valuable but not vice versa the apparent encounter rate is also affected and specialisation should then be preferred when

$$\frac{(1-\theta)\lambda_1 E_1}{1 + (1-\theta)\lambda_1 H_1} > \frac{\lambda_1 E_1 + \lambda_2 E_2}{1 + \lambda_1 H_1 + \lambda_2 H_2}$$

This favours generalisation under an even wider range of conditions as even fewer type 1 prey are taken by the specialist and the apparent value of type 2 increases

(see c in Fig. 4.1). If the less valuable prey are mistaken for more valuable prey and not vice versa, then the condition becomes

$$\frac{\lambda_1 E_1 + \theta\lambda_2 E_2}{1 + \lambda_1 H_1 + \theta\lambda_2 H_2} > \frac{\lambda_1 E_1 + \lambda_2 E_2}{1 + \lambda_1 H_1 + \lambda_2 H_2}$$

The benefit from specialising on type 1 will decrease as misidentification increases, as the predator will inadvertently take type 2 prey. Unlike the previous two inequalities, increasing misidentification will not favour generalisation. Thus the conditions for specialisation are the same as those for no misidentification (A in Fig 4.1).

Prey misidentification thus increases the optimum diet width whenever valuable prey are mistaken for less valuable prey. The model of Hughes (1979) also predicts that prey misidentification increases optimal diet width. Hughes's model acts through prey misidentification causing time to be wasted handling suboptimal prey which are subsequently rejected; the present model acts more fundamentally through misidentification affecting the predator's estimate of the profitability and availability of each prey, so that a wider diet is selected. Both mechanisms may act together but the relative importance of each is unknown. The mechanism involved in Hughes's model will have its greatest influence when handling is long

compared to the average interval between finding suitable prey. In the present model, the mechanism involved will have its greatest influence when handling time is short. In addition to increasing optimal diet width, prey misidentification will, in itself, obviously increase the range of prey taken.

It is easy to recognise those cockles which have been opened by oystercatchers since the last high tide. They have a characteristic position (anterior end upwards, valves separated by about 90^{o} and the shell slightly submerged), are surrounded by footprints where the bird has been struggling to prise open the valves and contain shreds of torn adductor muscle. All cockles were collected along a parallel series of transects, each two metres apart. Collection was either at low tide or once the oystercatchers had deserted a feeding site, whichever was the earlier. Checks failed to locate any more cockles, suggesting that there was no bias such as me noticing large ones more readily. All the collected cockles were aged and measured. The shells of cockles eaten at night were collected at dawn on days when dawn and low tide coincided.

For the sake of analysis, the cockles were divided into five size classes: 0-17.9mm; 18.0-21.9mm; 22.0-25.9mm; 26.0-29.9mm and 30.0+mm. The feeding rate for each site (see Chapter 5) was multiplied by the proportion of each size class taken to give the rate at which each size class was taken.

The pacing rate and the time it takes to make a peck were estimated by the method of Goss-Custard and Rothery (1976). The time oystercatchers feeding on cockles took to make forty paces was measured and the number of pecks made in that period was counted. The observation was abandoned if the oystercatcher extracted a cockle or the searching was disrupted. This was repeated at least forty times in each of 8 of the observation sites. Regression analysis was carried out on each set of data with the number of pecks as the independent variable and the time to take forty paces as the dependent variable. The slope is then the time it takes to take a peck and the intercept is the time it takes to make forty paces when no pecks are made.

(a) Size selection

In all sites the energy content of cockles increased exponentially with length (a typical example is given in Fig. 4.2). Mean handling time increased with mean cockle size taken (Fig. 4.3). Dividing the energy content by the handling time (from Fig. 4.3) gives an estimate of the profitability of each size class for that site. This shows that the largest cockles have the highest profitability (Fig. 4.2). Although the relationship between profitability and size varies between sites, in all sites studied the largest cockles had the highest profitability.

If oystercatchers behave according to optimal foraging theory they should prefer the largest cockles because they are the most profitable. Comparing those taken by oystercatchers with those present in the mud shows that oystercatchers do take a disproportionate number of large cockles (Fig.4.4 and Fig. 4.7). But this might be because large cockles are more available and so easier to find rather than because they are preferred.

Preference can be separated from availability if the feeding rate is measured over a range of prey densities. The preferred prey should be taken

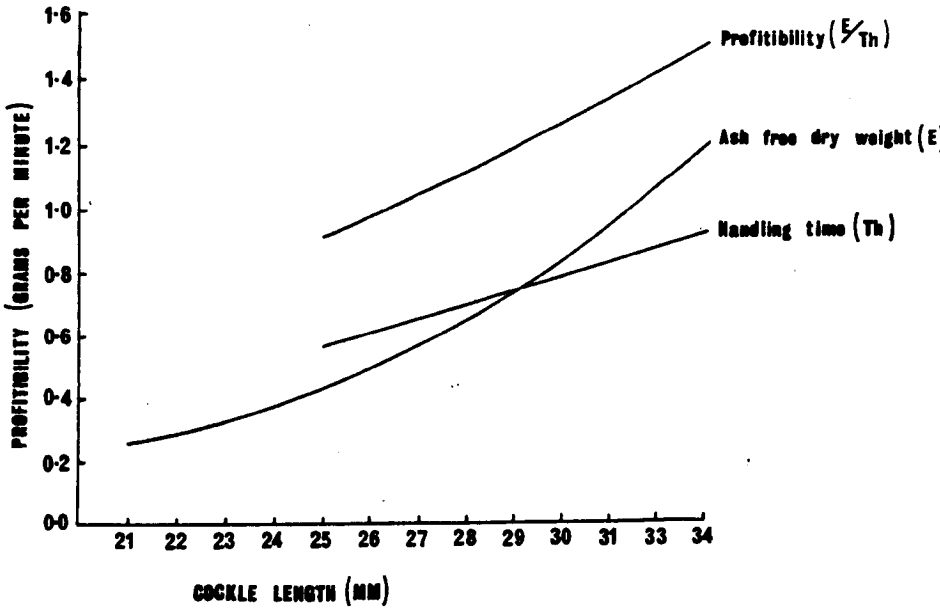


Fig. 4.2 Relationship between profitability (E/Th) and cockle length for site B.

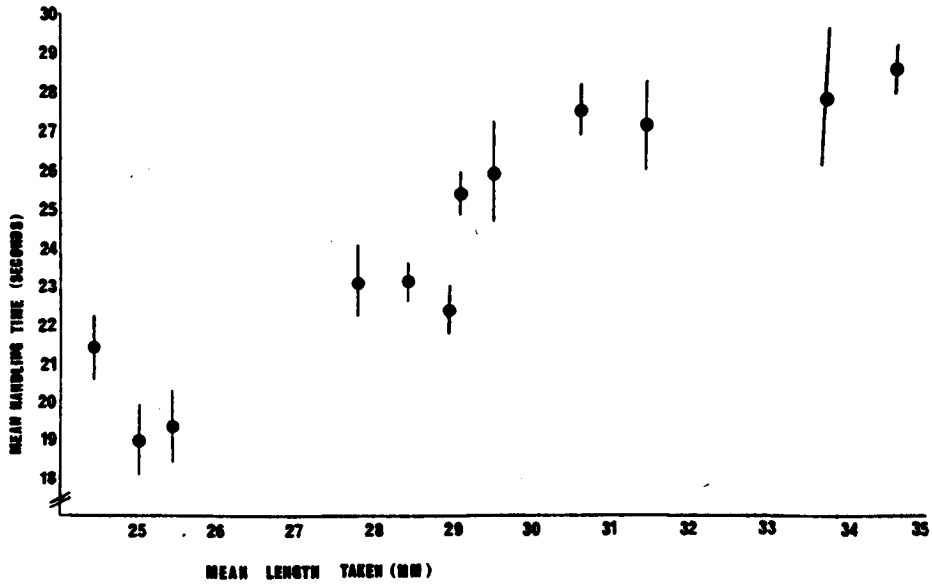


Fig. 4.3 Mean handling time in relation to mean size taken Each point refers to one observation site.

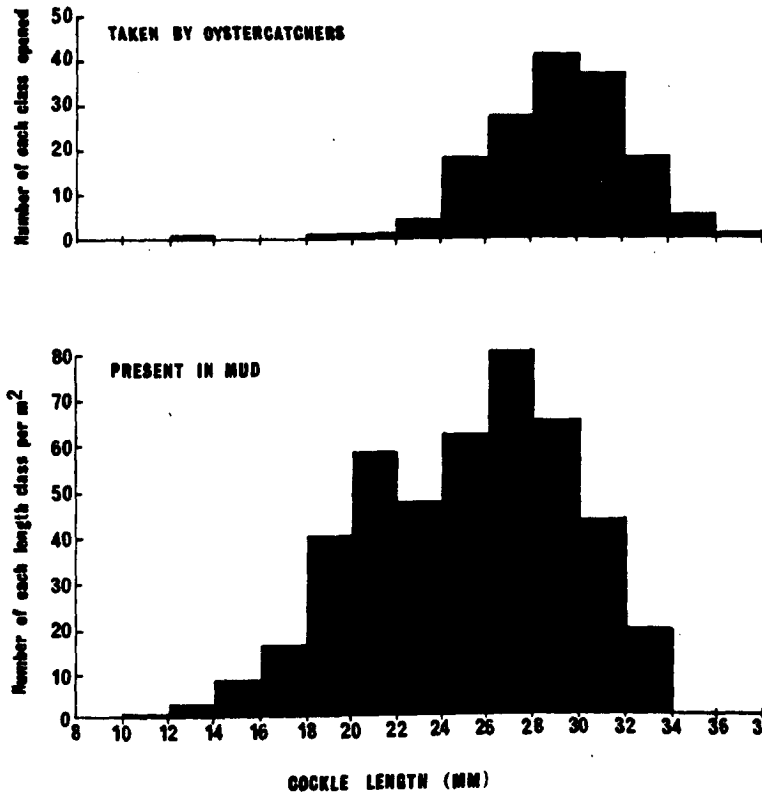


Fig. 4.4 The size of cockles taken by oystercatchers in site B and their density in the mud.

whenever it is encountered hence there should be a good correlation between the rate they are taken and their density in the mud. Less preferred prey may also be taken when few preferred prey are available and the density of less preferred prey may be irrelevant to their rate taken (see introduction). Hence a poor correlation is expected between the rate less profitable prey are taken and their density in the mud (Goss-Custard 1977a). Thus the correlation coefficient of the rate taken plotted against density in the mud can be used as a measure of preference.

Figure 4.5 shows the rate taken against density for the five size classes of cockles. The correlation coefficient increases with prey size (Fig. 4.6). This shows that the larger cockles are preferred. The largest cockle size class does not have the highest correlation coefficient, but the difference from the 26.0-29.9mm class is not significant ($p>0.1$). Larger cockles have a steeper relationship between rate taken and density (Fig. 4.6) which confirms that oystercatchers take a disproportionate number of large ones.

Some cockles were rejected once captured. Some of these appeared trapped on the end of the beak; the bird would then flick the beak so the cockle would fly off. The percentage rejected varied between 0 and

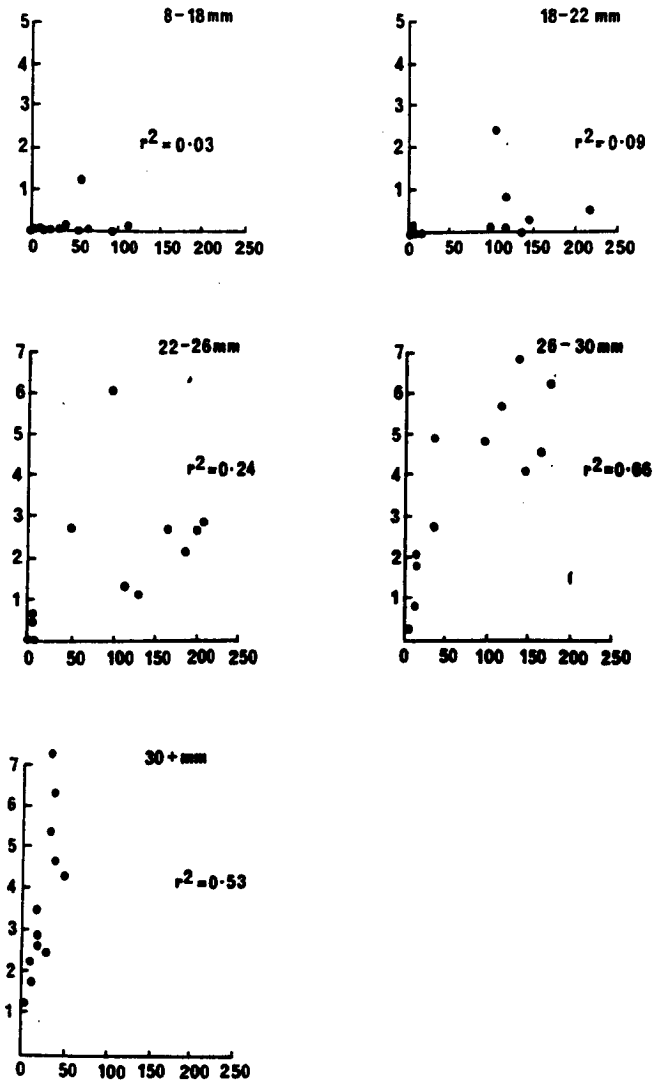


Fig. 4.5 The rate each cockle size is taken (per ten minutes searching) in relation to their density in the mud (per m^2) for each of five size classes.

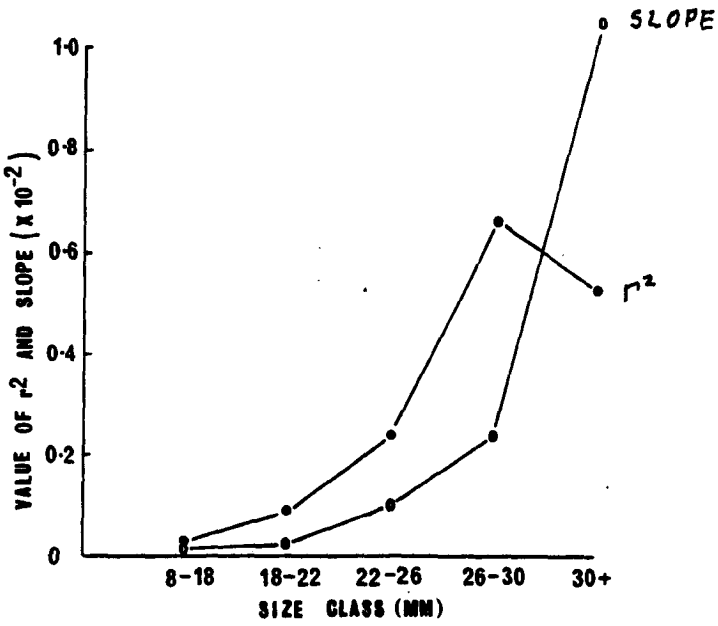


Fig. 4.6 The values of slope and r^2 for each of the graphs in Fig. 4.5 for each size class.

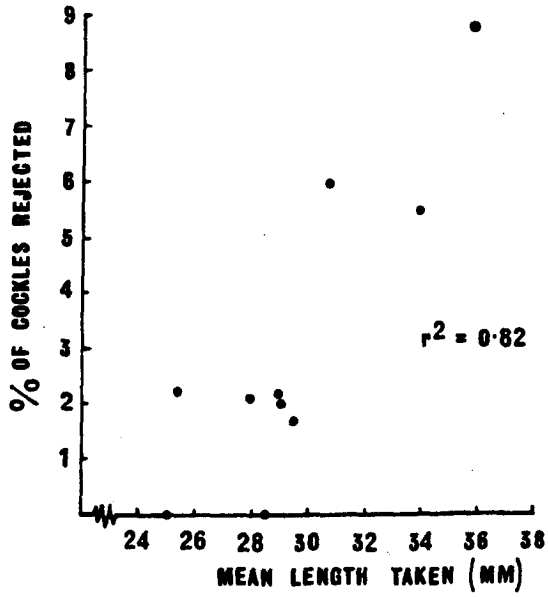


Fig. 4.7 The percentage of cockles extracted from the mud but then rejected in relation to mean size taken.

9% and increased with the mean size taken (Fig. 4.7), suggesting that the larger ones were more likely to be rejected. This might help explain why the largest cockles do not have the highest correlation coefficient between rate taken and density because the profitability of the large cockles will be reduced if many cannot be opened.

Optimal foraging theory states whether or not the less profitable prey is taken depends entirely upon the rate at which the more profitable prey are taken and not on own density. If data *are* expressed as numbers per unit time, we cannot distinguish whether few less profitable prey are taken because the predator is specialising on more profitable prey or because they are scarce. These explanations can be separated by expressing the results in terms of the risk of a cockle being taken by an oystercatcher that walked over it. Ideally risk would be expressed by dividing the number of cockles taken by the oystercatcher searching in a given area by the number of cockles in that area. This was not possible as the width of the oystercatchers search path was not known. However dividing the number of a size class taken (per linear metre searched) by the number of these cockles present in the mud provides an index of risk (Goss-Custard 1977a). Unfortunately search speed was only measured in 8 of the 12 sites.

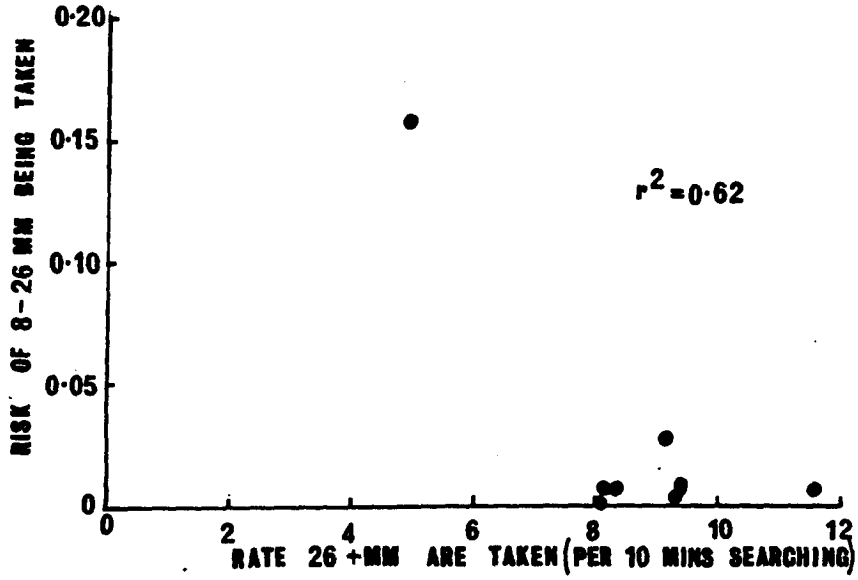


Fig. 4.8 The risk of small cockles (8-26mm) in relation to the rate large cockles (over 26mm) are taken per ten minutes searching.
Risk calculated as

$$\frac{\text{Rate 8-26mm taken per ten minutes searching}}{\text{Density of 8-26mm cockles per } m^2 \text{ x paces per second.}}$$

The effect of the rate at which large cockles are taken on the risk of a small cockle being taken is shown in Figure 4.8. The correlation is very unsatisfactory as it depends largely upon one point but it supports the prediction that the rate at which less profitable prey are taken depends upon the rate at which profitable prey are taken. The rate at which small cockles were taken appeared to have little effect on the risk of a large cockle being taken ($r^2 = 0.17$).

Contrary to most optimal foraging models, small cockles are taken more often as their density in the mud increases (Fig. 4.5).

Misidentification

In Hughes's (1979) model, the predator may include less profitable prey in the diet as its abundance increases. Hughes's models assumes time is wasted handling suboptimal prey which are subsequently rejected. The cockles seen to be rejected were probably the larger ones which were highly profitable yet could not be opened (Fig. 4.7). The decision of whether or not to attack a prey will be made when the beak is beneath the surface of the mud. If suboptimal prey hinder making this decision, then the time it takes to make a peck will increase in the presence of less profitable prey. The time to make a peck does increase with the

proportion of cockles under 22mm but the correlation is very poor (r^2= 0.18). Thus there is little evidence for time being wasted by misidentification.

In my model, the density of less profitable prey should have no effect on the rate at which they are taken (see introduction) so that cannot explain why small cockles are taken more often where they are more frequent. In addition to the effect on the optimal diet, misidentification may have simpler consequences. It is possible that oystercatchers mistake small cockles for large ones, and the rate at which they do this is likely to increase with the density of small cockles.

Night feeding

Observations with an image intensifier showed that oystercatchers fed as actively at night as during the day but their feeding rate was about half that found during the day (Chapter 8). The feeding behaviour also differed. During the day, oystercatchers walk slowly forwards, pecking at the ground. At night, they often use a sewing-machine like action. Hulscher (1976) found a similar change in behaviour in captive oystercatchers. This switch in behaviour suggests that oystercatchers feed by touch at night yet use some visual clues during the day. Further indications that they use visual clues during the day are that they sometimes reorientate themselves before pecking and

and that they take many paces between pecks.

Figure 4.9 shows that oystercatchers feeding at night take fewer large cockles than when feeding during the day. The means are significantly different ($p<0.001$). Visual feeding enables oystercatchers to find many of the large cockles (15% of the diet were larger than any I found in my 20 x 1/10 m^2 samples). During the night the sewing-machine action must reduce the number of large cockles that can be found.

The exponential increase in energy content with size makes these very large cockles highly profitable. Combining the data from Figure 4.9 with the curve of energy content against cockle length shows that the cockles taken at night have on average an energy content that is 25% lower than those taken during the day. In addition cockles are taken at half the daytime rate (Chapter 8), so the biomass intake during the night is 62.5% lower than during the day.

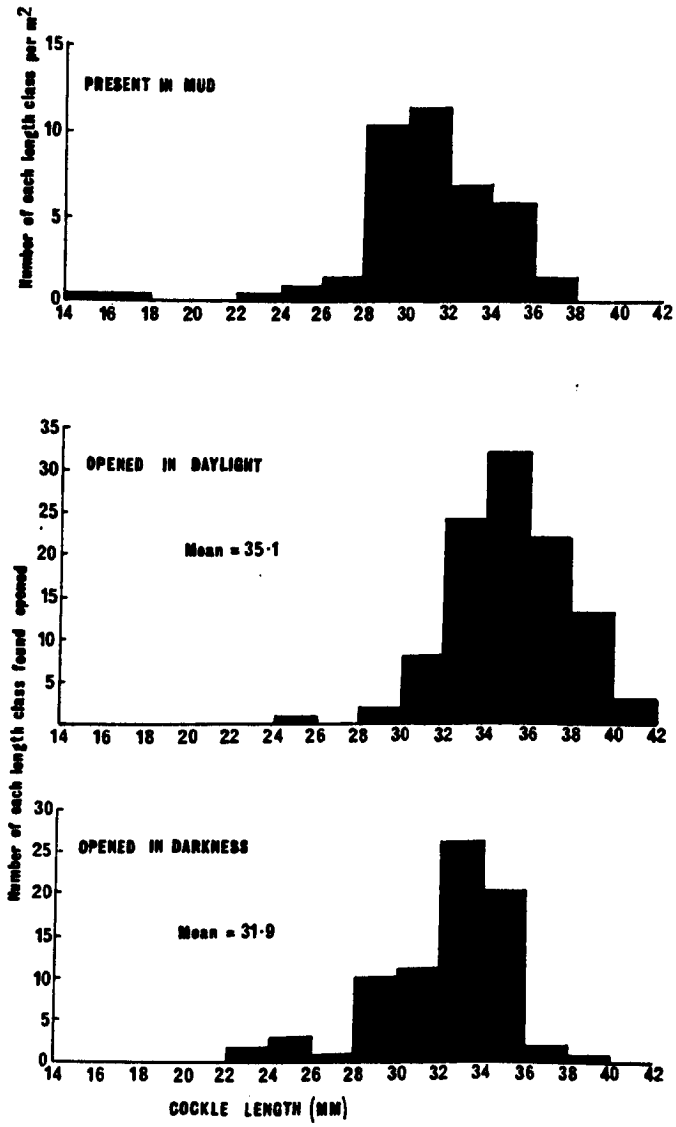


Fig. 4.9 The sizes of cockles taken during daylight and night in site C and those present in the mud.

DISCUSSION

The prediction that less valuable prey will be ignored if valuable prey are frequently encountered has been tested by Werner and Hall (1974) using bluegill sunfish Leponis macrochirius; by Krebs et al. (1977) using great tits Parus major; by Goss-Custard (1977a) using redshanks Tringa totanus and by Elner and Hughes (1978) using shore crabs Carcinus maenas. In each case the results agree with the prediction, as do mine although the correlation depends entirely upon one point.

In Elner and Hughes' (1978) study, less profitable prey were included in the diet as they became more abundant. This contradicts the predictions of most foraging models (e.g. Charnov 1976). Hughes (1979) suggested that this was in accordance with his misidentification model as the rejection time was not negligible. The results of this study are similar as the risk of a small cockle being taken declines as more large cockles were taken (although the evidence was unsatisfactory), yet the rate at which small cockles were taken increases as the density of small cockles increases in the mud. Unlike Elner and Hughes' study, rejecting small prey did not appear to take any significant time and so this behaviour cannot be explained by any present model. A possible explanation

is simply that oystercatchers mistake small cockles for large ones, and the rate at which they do this is likely to increase with the density of small cockles.

SUMMARY

Optimal foraging theory, which predicts the preferred size of prey and the range of prey types that should be taken, was extended to include the consequences of misidentification. There was little evidence for time being wasted by misidentification.

Profitability (energy content per second of handling time) increases with cockle size. The prediction that oystercatchers should prefer the larger, more profitable cockles, was supported by the birds' behaviour.

There was some evidence that the risk of small cockles being predated declined as the rate at which large cockles were taken increased. This is what is predicted by optimal foraging theory.

Oystercatchers use some visual clues to find prey during the day, but use only tactile clues at night. They took smaller prey at night, which in the site studied, had a flesh content 25% less than those taken during the day.

5. THE FUNCTIONAL RESPONSE

INTRODUCTION

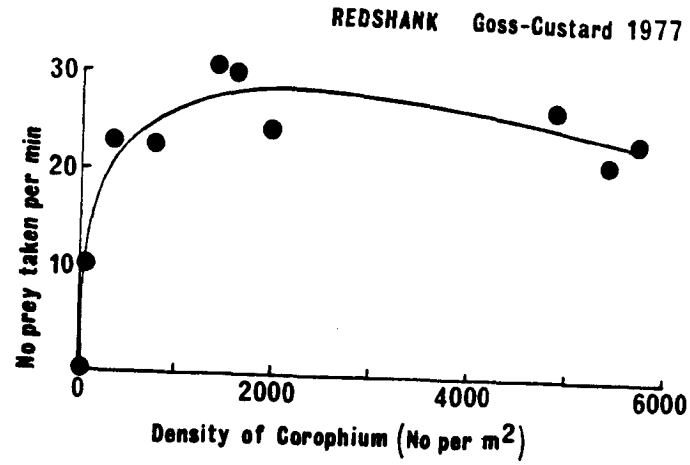
(a) Basic shapes of responses

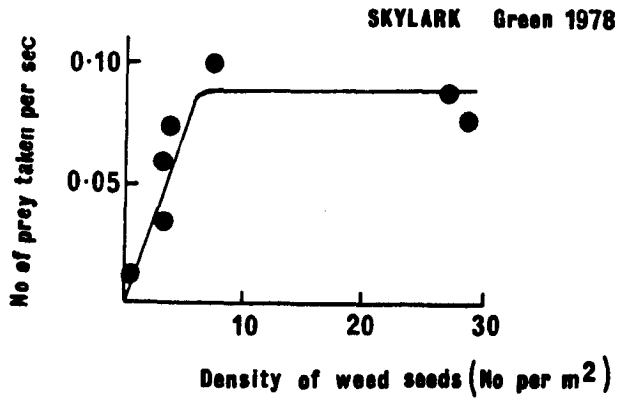
The relationship between the number of prey eaten by a predator and the density of available prey was first called the functional response by Solomon (1949). Holling (1959a) showed that the curves describing these responses were either sigmoid or a decelerating rise to an asymptote. In these studies, sigmoid curves (type III functional responses) were shown by vertebrate predators and asymptotic curves (type II functional responses) were produced by invertebrates. "Vertebrate" and "invertebrate" responses have even been used as synonyms for type III and type II responses respectively (Murdock 1973). It has since been suggested that sigmoid responses are actually widespread amongst invertebrate predators (Hassell et al.1977), so the terms type II and type III are now generally preferred.

The form of the functional response can vary according to whether or not alternative prey are present. In many studies, there has been an alternative prey present and the functional response has been type III (Holling 1959a; Royama 1970; Murdock and Oaten 1975). When the prey for which the functional response is being described ("studied prey") is scarce the predator

turns to the alternative prey. This "switching" has been widely recorded in both vertebrates and invertebrates (Holling 1959a; Ivlev 1961; Allen and Clarke 1968; Royama 1970; Manly-Miller and Cooke 1972; Krebs 1973; Lawton, Beddington and Bonser 1974; Murdock, Avery and Smyth 1975; Murdock and Oaten 1975), and produces a type III response as the predators disproportionately reduce their feeding on the studied prey once it is below a certain density. But if no alternative prey is present, the predator has to continue taking the studied prey at low prey densities so the inflection is removed and the functional response becomes type II. Figure 5.1 shows the functional responses for birds feeding on one prey type that I could find in the literature. In each case the response is a type II.

You can get a type III response if the predator stops feeding at low prey densities (Hassell et al.1977). But this is maladaptive in mobile animals which can move elsewhere. The houseflies used by Hassell et al. (1977) were restrained. In addition, at low prey densities it may have been difficult for the houseflies to realise that food was present in the feeding arena. Ceasing feeding when the prey density is low seems most likely to be worthwhile in sessile animals and so is not expected for oystercatchers.





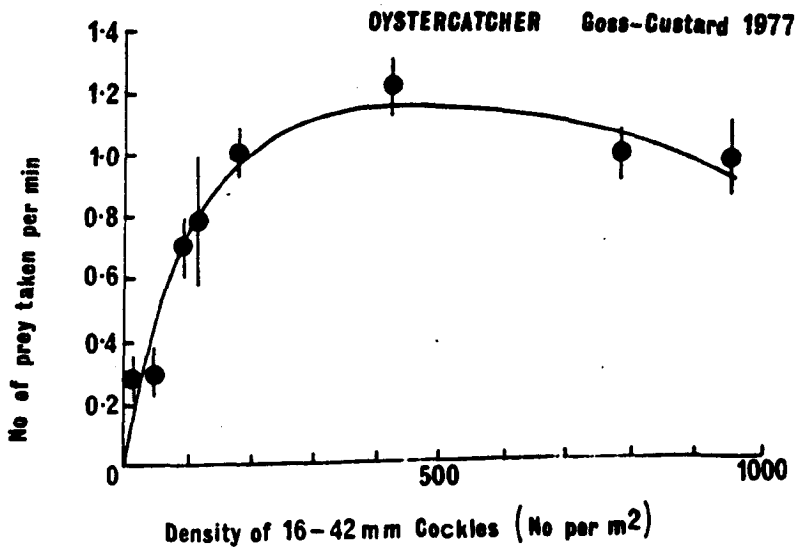


Fig.5.1 Functional responses of birds (continued over)

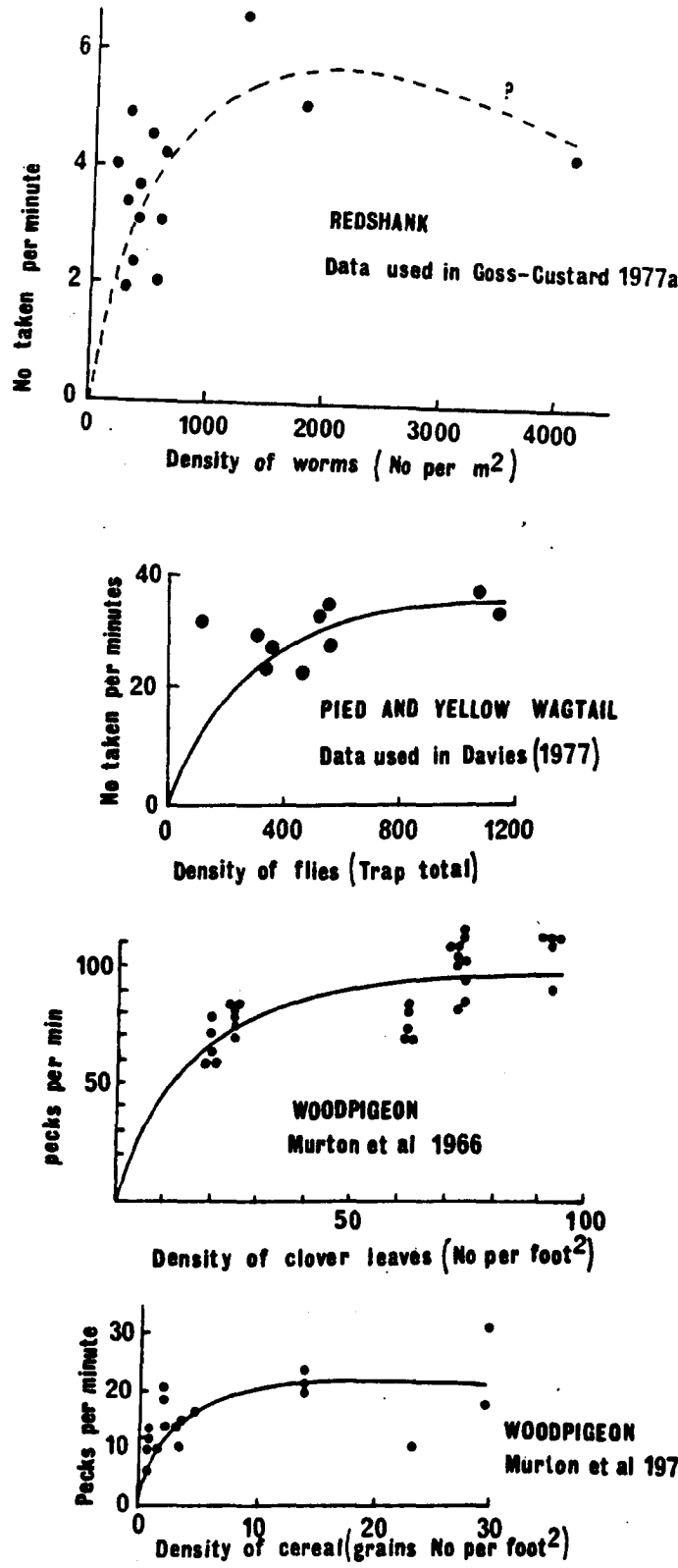


Fig.5.1 Continued. Functional responses of birds

(b) The level of the plateau

In studies of functional response, feeding rate is either expressed in terms of the number taken by a feeding predator during a short period or the number taken over much longer periods (e.g. 24 hours) including the time not spent feeding. In the first method, feeding rate is the rate at which a predator finds prey whilst actually foraging. This relationship is described by Holling's (1959b) "disc equation", so called because in his original experiment a blindfolded secretary searched for sandpaper discs on a table.

$$Na = \frac{a' \alpha_i T}{1 + a' \alpha_i Th}$$

where Na = the number of prey eaten

a' = the instantaneous attack rate

α_i = the prey density in the ith patch

T = the time spent searching

Th = the handling time

This equation predicts a level plateau when the predator spends practically all its time handling prey. However, in many laboratory studies it is common to determine the number of prey taken over a long period at each prey density simply by counting either the number missing, the number of parasitised prey or the number in the predator's gut. Once a threshold prey density has been reached when the predator can find all of its requirements, satiation must limit the

	PREY TAKEN PER DAY	PREY TAKEN PER MINUTE FORAGING
NO ALTERNATIVE PREY	TYPE II	TYPE II
	Plateau due to satiation	Plateau attributed to handling time
		Suggested also due to selection
ALTERNATIVE PREY PRESENT	TYPE III	TYPE III
	Inflection due to switching	Inflection due to switching
	Plateau due to satiation	Plateau due to selection, handling time and maintaining a varied diet.
USE IN POPULATION STUDIES	Determining temporal variation in mortality	Determining spacial variations in mortality.

Table 5.1. The functional response under different experimental conditions.

number of prey eaten and the curve levels off. The level of the plateau will then depend upon satiation. However, the disc equation is frequently applied to such experiments. This is incorrect because handling time cannot limit intake when so much time is spent loafing. The application of the disc equation here is meaningless.

Table 5.1 summarises the functional response under different experimental conditions. This classification seems as appropriate for invertebrates as for vertebrates. The table incorporates the suggestion that increased prey selection at high prey densities contributes to the plateau (see discussion). Holling (1959a) and Curio (1976) suggested predators attempt to maintain a varied diet if an alternative prey is present. This too will contribute to a plateau as even if the studied prey are very abundant the predator will seek out the alternative prey.

(c) Oystercatchers and cockles at Traeth Melynog

Oystercatchers at Traeth Melynog feed mainly on three prey types: cockles, Scrobicularia plana and worms (Scoloplos armiger, Nereis diversicolor and Arenicola marina). A few individuals feed on mussels Mytilus edulis and the balthic tellin Macoma balthica outside the study area. Inspection of mud samples (Rees and Walker 1978; pers obs) showed that no other important prey species was present (for comprehensive list of

prey species see Dare (1966) and Cramp and Simmons (Eds) in prep).

Individual oystercatchers are known to specialise, at least in the short term, on one prey species (Norton-Griffiths 1968; Dare and Mercer 1973). Of 121 hours detailed observation at Traeth Melynog, only on 4 occasions was more than one prey species taken within ten minutes. Since cockle specialists eat nothing else I expected the functional response to be type II.

The prey taken could be easily recognised as they were eaten by the following criteria:

Cockles: Handling time exceeds ten seconds. Extracted with bill inserted between valves so that cockle appears as round object at end of beak. Bird struggles whilst opening.

Scrobicularia plana: Often extracted from the mud with considerable difficulty, frequently from great depth (always much deeper than cockles), shell held between mandibles so appearing cigar shaped. Opened with less difficulty than cockles.

Worms: Handled rapidly (less than five seconds) and often seen.

Mussels: Similar to cockles but different shape may be detected if lifted up. Only taken on mussel beds.

Macoma balthica: Similar to S.plana but nearer the surface, smaller than cockles and opened easily. Best confirmed by presence of opened shells, but rarely taken, and then only near the high tide mark.

The relative frequency that each bivalve was taken varied over the beach. Checks showed that the trends in the apparent importance of each bivalve made through observations agreed with the trends in the actual importance determined from the opened shells lying on the surface. This confirmed that the prey

species taken could be separated by observation.

The feeding techniques for the three main types of prey are different and with practice each individual's prey specialisation could be identified without waiting for them to extract a prey. The criteria used were as follows.

Cockles: Shallow pecks used, bill inserted to about a tenth of its length. Birds often re-orientate themselves before pecking. May peck at empty or opened cockle shells. Twists head from side to side when attempting to enter cockle.

Scrobicularia plana: Bill inserted from half to full length. Peck over twice as frequently as worm and cockle feeders.

Worms: Beak inserted from quater to two-thirds length. Often pauses, appears to spot a prey a couple of meters away, runs, then immediately pecks at ground. Rarely hesitates before pecking.

This seperation proved accurate, as was shown by comparing the prey I thought the individual was searching for with the prey type subsequently seen being taken (Table 5.2).

Table 5.2 A test of my ability to identify a bird's specialisation from its searching behaviour

		PREY TYPE ACTUALLY TAKEN		
		Cockles	S.plana	Worms
SPECIALISATION ASSESSED BY SEARCHING BEHAVIOUR	Cockles	109	1	
	S.plana		23	2
	Worms		4	79

A series of observation sites were marked out on the mudflats with metal stakes (Fig. 1.1). Most observation sites were 100 meters square but one was 100 x 50 to standardise conditions within the site.

Oystercatchers were watched through a 15-60 x 60 telescope. A hide was not used as birds followed the tide and consequently spent little time in most observation sites. For each site, the number of cockles taken by an oystercatcher in ten minutes was recorded. Due to the difficulty of watching an oystercatcher and a stop watch simultaneously, some observations exceeded ten minutes, hence not all feeding rates are integers. The handling time for each cockle eaten was also noted. Handling time was measured as the time elapsing between my realising that the oystercatcher had found a cockle and the moment when the oystercatcher continued searching for prey or in some way change its behaviour. The distance between the observed bird and the water's edge was recorded at the begining of the ten minute observation period. These ten minute

observations were alternated with counts of the birds present within the site (see Chapter 8). All observations were dictated into a portable tape-recorder. As many sets of observations were made as was possible whilst the birds were within the observation site. The data for each site were collected within one of three two month periods: November-December; January-February; March-April. Some sites were studied for more than one period of two months. Hence some of the points on the graphs refer to observations at the same site for different two month periods.

The methods used for estimating the cockle density in each site is described in Chapter 1. Unless otherwise stated, cockle density refers to the density of all cockles that were retained by a 7 x 7 mm sieve.

(1) Changes over the tidal cycle

Figure 5.2 shows the feeding rate in site A as the tide flows away from the observation site. There is no change in feeding rate. A series of t tests showed that for each site the feeding rate on the ebb and flood tide did not differ ($p<0.05$). Thus observations from all stages of the tidal cycle can be combined.

(2) The shape of the functional response

Figure 5.3 shows the functional response obtained for oystercatchers feeding on cockles at Traeth Melynog. The number of cockles taken in ten minutes increases rapidly as cockle density increases up to a density of approximately ninety cockles per square metre. After this, the number taken increases only slowly. This approximates a type II functional response.

As noted earlier, Holling's disc equation produces a plateau because so much time is spent handling prey at high prey densities. Does this equation predict the behaviour of oystercatchers at Traeth Melynog? Figure 5.4 shows the functional response when the feeding rate is expressed in terms of the search time where the search time is the total observation time minus the total handling time (i.e. T-Na Th). If handling time alone determines the plateau, this

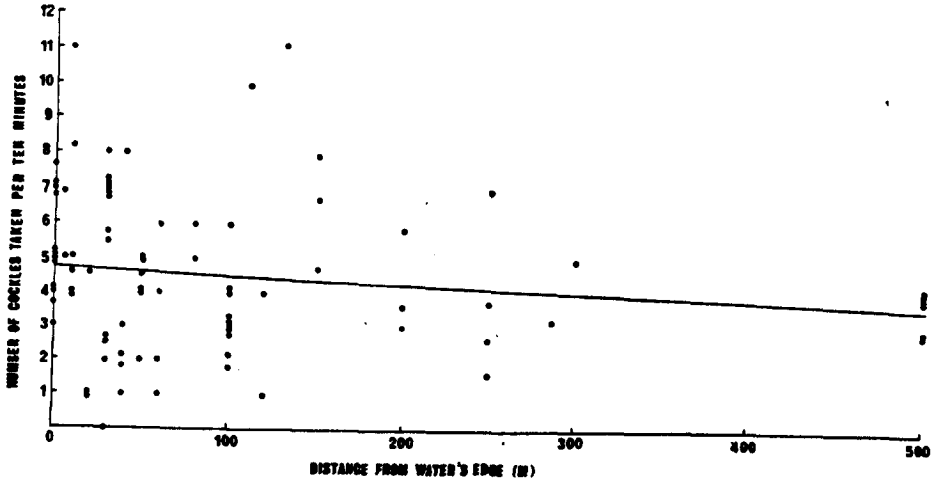


Fig. 5.2 The feeding rate in site A in relation to the distance between the feeding bird and the water's edge. All observations on ebb tide.

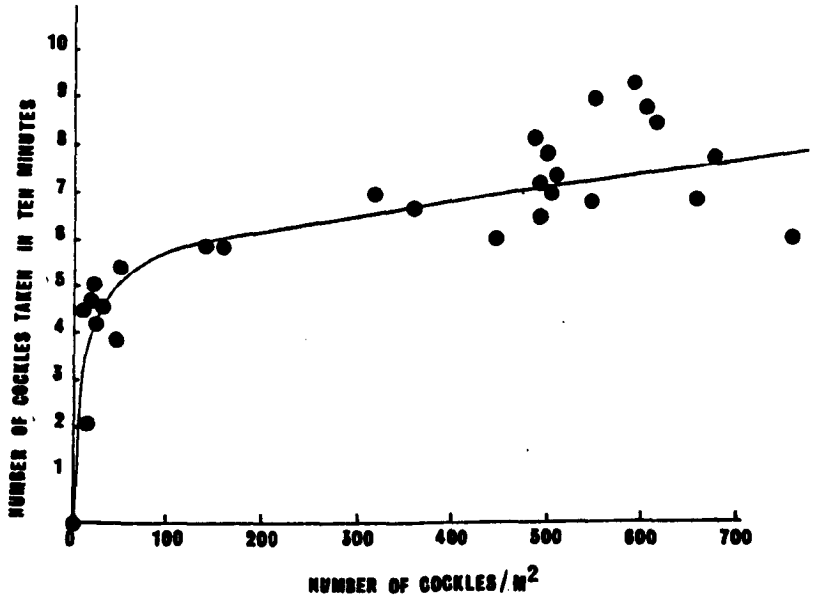


Fig. 5.3 The number of cockles taken per ten minutes in relation to cockle density.

relationship should be linear and pass through the origin as illustrated by rearranging the disc equation

$$\frac{Na}{T - Na\ Th} = a' \alpha_i \qquad (2)$$

The slope will then be a' - the instantaneous attack rate. However it is still clearly curvilinear (Fig. 5.4) and the response was not greatly affected by the removal of handling time. This shows that handling time is not solely responsible for producing the type II functional response.

This conclusion is confirmed by analysing the data a different way. By adjusting the values of a' and Th the disc equation can describe any asymptotic curve. But if the derived value of Th differs from the value measured directly, then this shows that the disc equation is an inappropriate description of the functional response. The value of the handling time (Th) can be derived by inverting the disc equation so

$$\frac{T}{Na} = \frac{1 + a' \alpha_i Th}{a' \alpha_i} \qquad (3)$$

then

$$\frac{T}{Na} = \frac{1}{a' \alpha_i} + Th \qquad (4)$$

Thus if the reciprocal of the feeding rate (i.e. $\frac{1}{Na/T}$ which equals T/Na) is plotted against the reciprocal of the prey density ($1/\alpha_i$) then the intercept will be the handling time (Th) and the slope will be the reciprocal of the

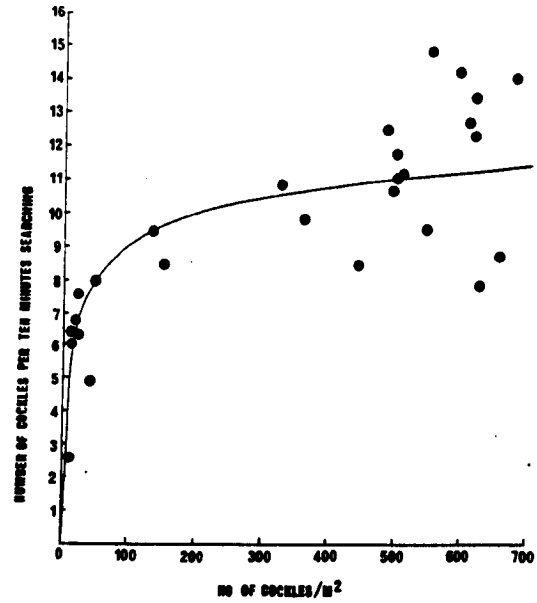


Fig. 5.4 The number of cockles taken per ten minutes searching in relation to cockle density.

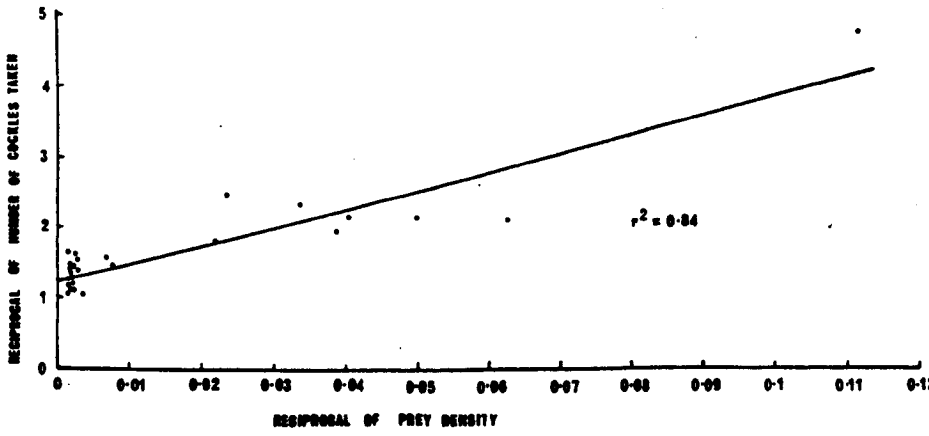


Fig. 5.5 The reciprocal of the number of cockles taken per minute against the reciprocal of prey density. The intercept is the predicted handling time.

instantaneous attack rate ($\frac{1}{a'}$). This method avoids many of the statistical problems that affect the method proposed by Holling (1959b). I am very grateful to Dr. Clive Anderson of Sheffield University for suggesting this analysis.

Figure 5.5 shows the reciprocal of feeding rate (i.e. T/Na) plotted against the reciprocal of the prey density. While this method of analysis emphasises points at low prey densities, it gives an estimate of the handling time as 1.29 minutes and the attack constant as 26.2 minutes. The actual handling time was between 19 and 29 seconds (Fig 4.3). Clearly the disc equation does not predict oystercatcher behaviour very well and the asymptote is not derived solely from handling time.

It could be argued that the poor fit of the data to the disc equation is due to the inclusion of size classes that the predators ignore. Oystercatchers may take a lower proportion of the prey at high prey densities simply because fewer of the prey are suitable. Feeding rate (expressed in terms of search time) was therefore plotted against the density of those above 22mm (Fig. 5.6). Although showing considerable scatter, it is evident that the relationship is not a straight line passing through the origin as predicted by the disc equation (equation 2). To confirm this, a regression analysis

was carried out which produced the line shown in Figure 5.6. The intercept is 6.7 $\pm$ 2.5, well above the origin. This confirms that the poor fit to the disc equation is not solely due to the inclusion of all size classes.

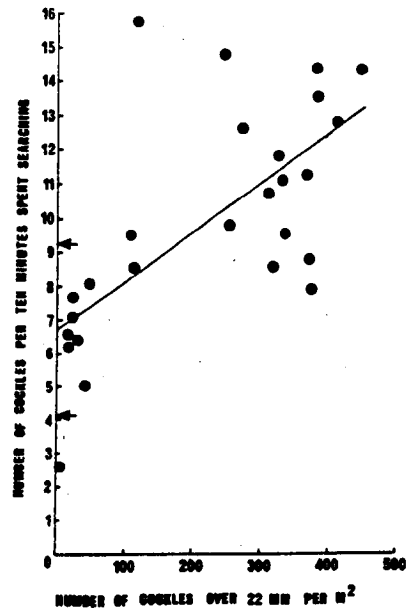


Fig. 5.6 Number of cockles taken per ten minutes in relation to the density of cockles over 22mm.

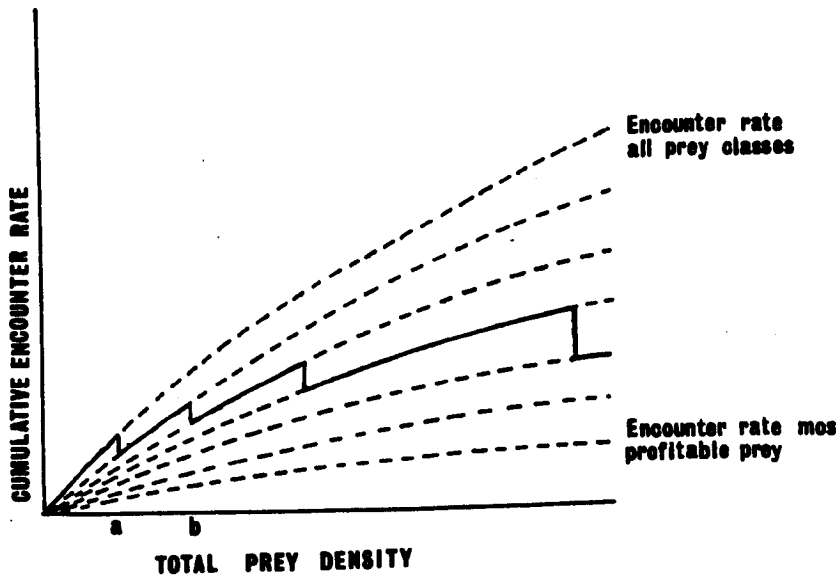


Fig. 5.7 Model of functional response. See text for explanation.

(a) Does handling time, satiation or prey size determine the asymptote ?

Clearly handling time is not solely responsible for producing the type II functional response as the response is still asymptotic once the effect of handling time has been removed (Fig 5.4). For handling time alone to have been responsible for the relationship in Figure 5.3, handling time would need to be about 1.27 minutes, three times greater than the observed.

A type II functional response would be produced if the predators are less hungry at high prey densities and feed more slowly. As argued above, this is most likely to occur if feeding rate is expressed in terms of numbers per day rather than numbers per minute foraging. If satiation affects feeding rate, then the feeding rate ought to vary according to how long they have been feeding for. Since oystercatchers cannot feed at high water, a decline in feeding rate might be expected over the tidal cycle. There is no evidence that foraging oystercatchers feed slower when the tide was flooding so satiation is probably unimportant.

The asymptote could be due to oystercatchers ignoring small prey, which form a large proportion of the high prey densities. If oystercatchers respond just to large prey then an analysis using all prey

classes could produce an asymptote - with fewer prey taken at high prey densities purely because there are fewer worth taking. Restricting the prey density to large prey appears to improve the fit to the disc equation (compare Figure 5.6 with Figure 5.3), suggesting the variations in size composition of the prey is partly responsible for producing the type II response.

Figure 5.6 allows for prey size and handling time yet still deviates considerably from a linear relationship passing through the origin. It thus appears that the combination of handling time, satiation and prey size is insufficient to explain the asymptote in the functional response.

(b) Comparisons with other studies

Table 5.3 gives the estimates of handling time and attack constant derived from the disc equation for all the functional responses shown in Figure 5.1. In each case, the time spent handling prey greatly exceeds the observed values. Multiplying the estimated handling time by the maximum feeding rate (from the line fitted to the functional response) gives the estimated total time spent handling prey (Column 6 Table 5.3). In many cases over 100% of the the time would be spent handling prey, further showing that the estimates based on the disc equation are unrealistically high. It is clear that the level

SPECIES	ESTIMATE OF a'	ESTIMATE OF Th (Mins)	r^2	n	MAX NO TAKEN	MAX % Th	STUDY
Oystercatchers and cockles	26.2	1.27	0.84	27	0.7	89%	This study
Oystercatchers and cockles	58.6	1.00	0.75	8	1.15	115%	Goss-Custard 1977b.
Woodpigeons and grain	0.2	0.034	0.64	15	23	78%	Murton et al 1963
Woodpigeons and clover	58.5	1.00	0.52	32	100	10,000%	Murton et al 1966
Redshanks and Corophium	78.4	5.43	0.86	9	28	152%	Goss-Custard 1977c
Redshanks and worms	29.0	0.22	0.16	14	5.8	128%	Data used in Goss-Custard 1977a
Wagtails and flies	0.2	0.034	0.01	10	34	133%	Data used in Davies 1977
Skylarks and seeds	1.31	0.09	0.81	7	5.1	46%	Green 1978

Table 5.3. Estimates of the handling time (Th) and the instantaneous search rate a' derived from fitting the disc equation to the functional responses of birds feeding on one prey. The maximum % of time spent handling prey is calculated by multiplying the maximum feeding rate by the estimated handling time and expressing this as a percentage of the time available.

of the asymptote is not caused solely by the time spent handling prey.

Satiation is probably not responsible for the plateau in feeding rate because ingestion rate varies greatly even though the number of prey taken is approximately constant. If satiation had been important, the rate of biomass intake would be constant, instead of increasing with prey density. Both redshanks feeding on Corophium and oystercatchers feeding on cockles on the Wash showed a type II functional response, yet each took a greater biomass at high prey densities (Goss-Custard 1970a, 1977b). Furthermore, redshanks feeding on worms do so in a manner which maximises their rate of food intake (Goss-Custard 1977a) yet show a type II functional response. The capacity of their stomach cannot limit the rate at which they eat Corophium since redshanks can eat a greater biomass of worms that they eat of Corophium over the same time period (Goss-Custard 1977c). Clearly neither handling time nor satiation provide sufficient explanation of the level of the asymptote either for the oystercatchers at Traeth Melynog or for other studies, and some other explanation is required.

(c) The foraging model

What sets the level of the plateau of the functional response if handling time and satiation do not? In this section I explore the possibility that

the selection of prey of different size classes may provide an adequate explanation. I base my argument on models of foraging behaviour which assume that predators choose diets that maximise the net yield of energy per unit foraging time (Emlen 1966; Schoener 1971; Timmin 1973; Pearson 1974; Pulliam 1974; Werner and Hall 1974; Charnov 1976; Eastabrook and Dunham 1976). Tests, in both theory and laboratory, have shown that the theory provides a reasonable description of the predators' behaviour (for review see Pyke et al. 1977; Krebs 1978). Does a model based on the theory generate asymptotic functional responses?

I have developed a simple graphical model shown in Figure 5.7. The prey are divided into size classes, which are ranked according to profitability (defined as the energy per unit handling time). If the handling time is ignored then the rate at which each prey class is encountered will increase linearly with prey density, but when handling time is incorporated the encounter rate is a curve determined by the disc equation (Fig. 5.7). The dependent axis of Figure 5.7 is then the encounter rate of all prey exceeding a certain profitability.

Optimal foraging theory states that all the prey that are encountered should be eaten when the prey is scarce. Thus at low prey densities the rate at which prey are eaten (thick line) is the same as the total

encounter rate (upper dashed line). The same theory predicts that whether or not the least profitable prey are taken depends entirely upon the abundance of the more profitable prey types. Thus, once a threshold level (say a) is reached, the least profitable prey is no longer taken. By the same argument, the second least profitable prey will be excluded from the diet once the abundance of the more profitable prey reaches a higher level (say b). Further specialisation will occur as the prey density continues to increase. The model produces a saw-toothed curve because predators behaving according to optimal foraging theory eat either all members of a prey class encountered, or none of them. However, in reality prey classes will often not be discrete (e.g. size classes), and such all or nothing responses have not been found in the predators studied (Krebs et al. 1977; Goss-Custard in press a). This will have the effect of smoothing out the expected functional response. Thus as the density of all prey sizes increases, specialisation on the most profitable prey results in less profitable prey being ignored and a type II functional response is produced.

The model assumes that the most profitable prey are also the largest prey eaten by the predator. This was correct at Traeth Melynog and for those studies in Figure 5.1 where this was investigated (Goss-Custard 1977a,b,c) but was not correct in other studies by

Davies 1977 and Elner and Hughes 1978. More studies are needed to see if this assumption is generally true.

The major assumption of the model is that the rate at which the less profitable prey are taken depends upon the density of the more profitable prey. This prediction has been confirmed both in the field and in the laboratory (Werner and Hall 1974; Davies 1977; Goss-Custard 1977a, in press a; Krebs et al. 1977) and there is some evidence for it for the oystercatchers at Traeth Melynog (Chapter 4).

However, the model assumes that the proportion of each size class does not vary with density, and this is not true at Traeth Melynog: there are a higher proportion of large prey at low prey densities (Fig. 3.5). This prevented a rigorous testing of the model.

Oystercatchers on the Wash show little increase in feeding rate with prey density yet their biomass intake increases due to increasing specialisation (Goss-Custard 1977b): this is entirely in accordance with this model. Thus I conclude that optimal foraging can contribute towards producing type II functional responses.

SUMMARY

The shape of the functional response depends more upon the experimental conditions than on the species involved. Type III responses are produced if an alternative prey is present. With only one prey species the response will be type II. Whether the predator is a vertebrate or invertebrate is irrelevant. It is stressed that fitting the disc equation is only justified if the feeding rate is expressed as the number taken whilst searching, not the number taken per day.

Oystercatchers at Traeth Melynog showed a type II response to the density of cockles. This was not due entirely to handling time (contra Holling 1959b). The correlations between the parameters of the cockle population also had some effect in producing the plateau, but handling time and satiation combined were insufficient to explain the asymptote of the functional response.

Analysis of other studies of bird functional responses show that all conform to a type II response yet handling time cannot be solely responsible for producing the plateau and satiation appears unimportant.

A model is described which is based on optimal foraging theory. It generates type II functional responses due to increased specialisation at high prey densities. Due to correlations within the prey parameters at Traeth Melynog, it proved impossible to apply this model to the data - although the foraging behaviour of the oystercatchers conformed with the model. Studies of oystercatchers feeding on cockles on the Wash (Goss-Custard 1977b) fit the predictions of the model.

6. THE AGGREGATIVE NUMERICAL RESPONSE

INTRODUCTION

The change in predator density with prey density is important in determining the pattern of mortality inflicted upon the prey population (Solomon 1949). This numerical response is the combination of two factors: the movement of predators between areas and changes in their survival and fecundity. These will be referred to as the aggregative numerical response and the population numerical response respectively. Crawly (1975) proposed that aggregation would be of overriding importance in determining the numerical response (this point is discussed further in Chapter 7). Since data from many seasons are required to describe the population numerical response, two seasons data from Traeth Melynog is insufficient so only the aggregative numerical response could be studied.

Although the importance of the aggregative numerical response has been appreciated for some time, there have been very few studies, especially when compared with the plethora of studies of the functional response. Notable exceptions are the work of Goss-Custard (1970a), Tinbergen (1976) and Hassell (1980). Three factors probably account for this lack of studies: firstly predator distribution depends upon many factors,

such as food availability, the physical environment, the direction of currents of air or water, disturbance and competition from other predators. It is therefore likely that the aggregative numerical response can only be realistically determined in the field, unlike the functional response which lends itself to laboratory experiments. Secondly, the relative contribution of the aggregative and population numerical responses may be hard to assess. Thirdly, the aggregative numerical response has not had a theoretical framework, equivalent to the disc equation for functional responses - on which such studies can be based.

(a) The ideal free distribution

Recent theory argues that the distribution of predators over a spacially variable food will be the outcome of the interaction of two opposing influences: food should be easier to find at high prey densities, so the predators will go there, but interference will be greater at high predator densities so the predators may try to avoid this by moving away (Hassell and May 1974). If we assume that predators always respond so as to maximise profitability (Krebs 1978), it is possible to describe the predator distribution taking into account the opposing effects of food density and interference; the result has been termed the ideal free distribution (Fretwell and Lucas 1970). I intend to show the application which the ideal free distribution has

in predicting aggregative numerical responses.

The concept of the ideal free distribution was developed by Fretwell and Lucas (1970) to account for the distribution of breeding birds; a similar argument was independently proposed by Parker (1970; 1974) to describe the distribution of dungflies Scatophaga stercoraria searching for mates. Fretwell and Lucas called the resultant distribution the ideal free distribution as it assumes the organisms are ideal in their judgement of the profitability of each habitat, and the organisms are free to move between habitats. This model can equally be applied to the distribution of foraging animals by assuming each tries to maximise its own food intake.

When the number of predators is low, the predators feed only in the best habitat (see Fig. 6.1) because profitability is highest there and there is no interference from other predators. As predator numbers increase, interference will reduce the profitability in the best habitat until it is equal to that in the intermediate habitat (Fig. 6.1). Predators should then feed in both habitats because the profitabilities are the same. If more predators arrive, then the profitabilities of both habitats will be reduced to that of the poorest habitat, and they should then feed in all three habitats. Thus, if the ideal free distribution is obeyed, all predators

should be in habitats with the same profitabilities and all should have the same feeding rate.

There are some reasons for believing that predators behave in ways likely to result in an approximately ideal free distribution. Most predators studied so far aggregate in areas of high prey density (for review see Curio 1976) yet avoid each other to avoid interference (see Hassell 1978). Amongst waders, birds also congregate where food is densest (Goss-Custard 1970a,1977c; Heppleston 1971; Prater 1972; O'Connor and Brown 1977; Bryant 1979), yet the proportion of predators in the areas of highest prey density depends upon the amount of interference. Goss-Custard (1970b,1976) showed that waders that detect food by sight were the most suscept ble to interference and so were the most dispersed. Those waders which fed by touch had little interference and thus fed close together. This pattern was preserved amongst conspecifics feeding on different prey e.g. redshanks flock when feeding by touch on Hydrobia yet are dispersed when locating Corophium by sight. Secondly, tests of optimal foraging theory show that predators can allocate their time in a manner which maximises their food intake (for reveiws see Pyke et al.1978; Krebs 1979). Finally, the ideal free distribution is an evolutionary stable strategy (see Maynard Smith and Price 1973) so behaviour that contradicts the ideal free distribution should be selected against, other things

being equal. With these tendencies, predators may therefore be expected to occur in an ideal free distribution.

(b) The model of the aggregative numerical response

Although mate selection in dungflies has been modelled and found to conform with the ideal free distribution (Parker 1970,1974), no generalised model exists for predators foraging ideally. It was therefore necessary to create a suitable model. This model assumes that the profitability of each habitat depends upon only two factors: the prey density and the interference caused by other predators present. Fortunately, both of these factors have been described mathematically.

The number of prey found (Na) in time T at each prey density (α_i) can be described by the disc equation (Holling 1959b).

$$Na = \frac{a'\alpha_i T}{1 + a'\alpha_i Th} \qquad (1)$$

where a' is the instantaneous search rate, and Th is the time it takes to handle a prey item. Hassell and Varley (1969) showed that the effect of predator density (b_i) on the searching efficiency (a) is

$$a = Q\, b_i^{-m} \qquad (2)$$

where m expresses the degree of interference and Q is the "quest constant". The value of these are calculated by plotting Log searching efficiency (a) against Log

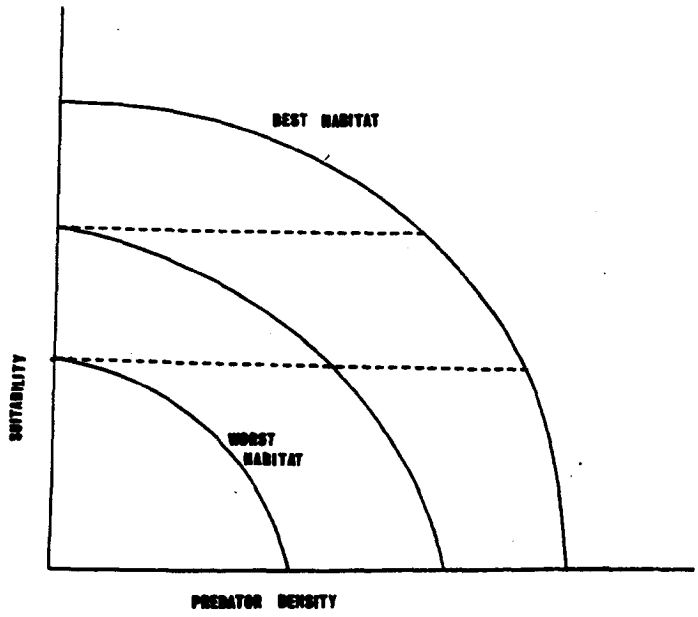


Fig. 6.1 The ideal free distribution (after Fretwell and Lucas 1970). For explanation see text.

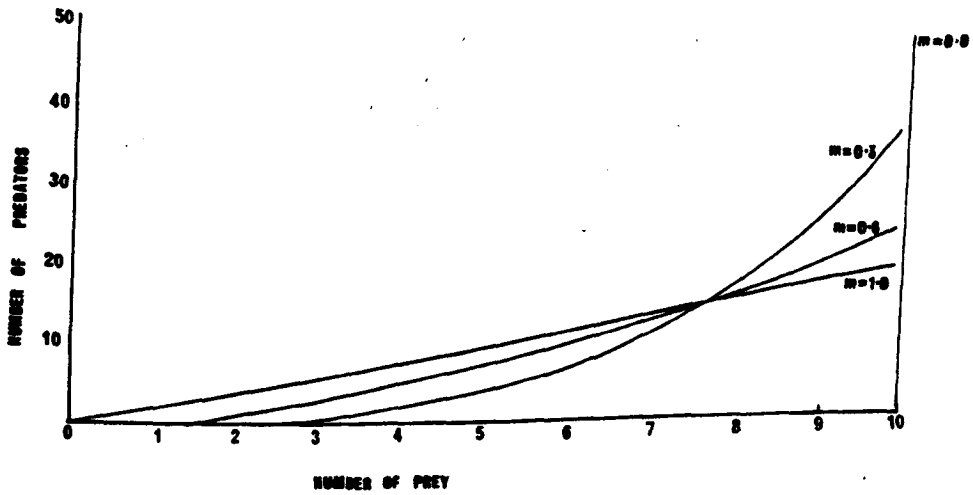


Fig. 6.2 The aggregative numerical response for different levels of interference assuming $b_i = k \alpha_i^{1/m}$

predator density (b_i); the resulting slope is m and the intercept is Log Q. As a = a'Ts, where Ts is the time available for searching, equation (2) can be incorporated into the disc equation (1) where upon

$$Q\, b_i^{-m} = \left(\frac{Na/T}{1 - (Na/T)\, Th} \right) \frac{Ts}{\alpha_i} \qquad (3)$$

(see appendix 1 for derivation). The quest constant and the handling time (Th) are both constants. If the ideal free distribution is obeyed, prey will be taken at the same rate (Na/T) by each predator, regardless of prey density, so that Na/T will also be a constant. Ts is the time left for searching after handling time is removed (i.e. Ts = T - Th Na). The ideal free distribution predicts that the same number of prey will be taken in a given time at each prey density, so that Ts is also a constant. Q, Th, Na/T, and Ts may all be replaced by a constant.

Hence $b_i = k\, \alpha_i^{1/m}$ (4)

where k is a constant.

The predator distribution can then be expressed purely as a function of prey density and the severity of the interference. Figure 6.2 shows the predicted aggregative numerical response for different values of the interference constant m. Published values of m vary between 0 and 0.96 (Hassell 1978).

The model has assumed that the relationship

between Log a and Log predator density is linear. In several studies, this relationship has been curvilinear so that m increases with predator density (Bakker et al. 1967; Burnett 1958; Ullyett 1949). Such curvilinear responses are expected as there must be a predator density below which predator interference is negligible and, therefore where the searching efficiency will be independent of predator density (Royama 1971; Rogers and Hassell 1974). This will make the expected numerical response more concave.

(c) Consequences for density dependence and stability

What effect would predators behaving this way have on the pattern of predation inflicted on the prey? The model predicts that when the interference constant m equals one the relationship between the number of predators and the number of prey is linear (Fig. 6.2). There is the same ratio of predators to prey at each prey density. The ideal free distribution also states that the prey are taken at the same rate at each density. Thus, when m=1, the same proportion of prey are taken at each prey density: the mortality inflicted by the predator is density independent.

When m is less than one the model predicts that there will be more predators per prey at high prey densities than at low - the mortality will be density dependent. Thus the model predicts that the degree of

interference dictates the strength of the density dependence.

If the ideal free distribution is obeyed, then the aggregative numerical response depends entirely upon the degree of interference. Hassell and May (1973) proposed an aggregation constant (μ) which describes, for a series of prey densities, the relationship between the number of predators (b_i) and the number of prey (α_i). This relationship was assumed to be

$$b_i = k\ {}_i{}^{\mu} \quad (5)$$

where k is a normalisation constant such that the b_i values sum to unity. This has the same form as equation 4 making it evident that $\mu = 1/m$. The consequences of this on the stability of predator-prey systems can now be investigated. Hassell and May (1973) showed that both the predator aggregation (μ) and the interference (m) increase stability. As $\mu = 1/m$ these are mutually exclusive: a species in which the individuals severly reduce their neighbour's fitness is unlikely to be one in which the individuals aggregate. The conditions for stability can be shown by replacing μ by 1/m in equation 31 (model 3) in Hassell and May (1973). Thus

$$Ns = Nt \sum_{i=1}^{n} \left[a' \exp(-Q\ (c\ a'^{\,1/m}\ Pt)^{\,1-m})\right] \quad (6)$$

where Ns = Surviving prey after parasitism

Nt = Total population of prey

Pt = Total population of predators

The stability boundaries for this equation are shown in Figure 6.3. The wide set of conditions under which the system is stable is due to the system being stabilised by aggregation when the interference is small, and by interference when m is large. The system is more stable when m is high (and stabilised by interference) than when m is low (and stabilised by aggregation). Thus interference still increases stability, despite the disrupting effect it has by reducing aggregation.

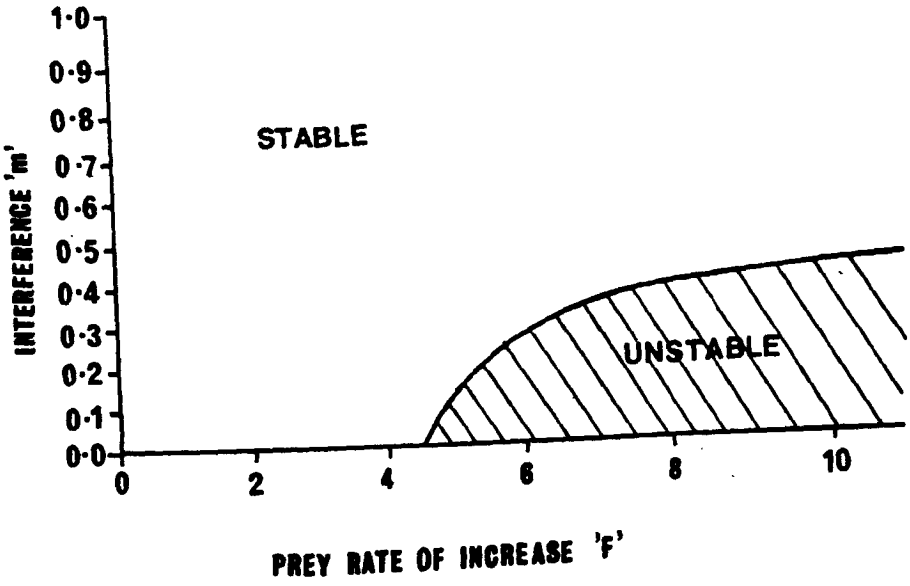


Fig. 6.3 The stability boundaries derived from equation (6)

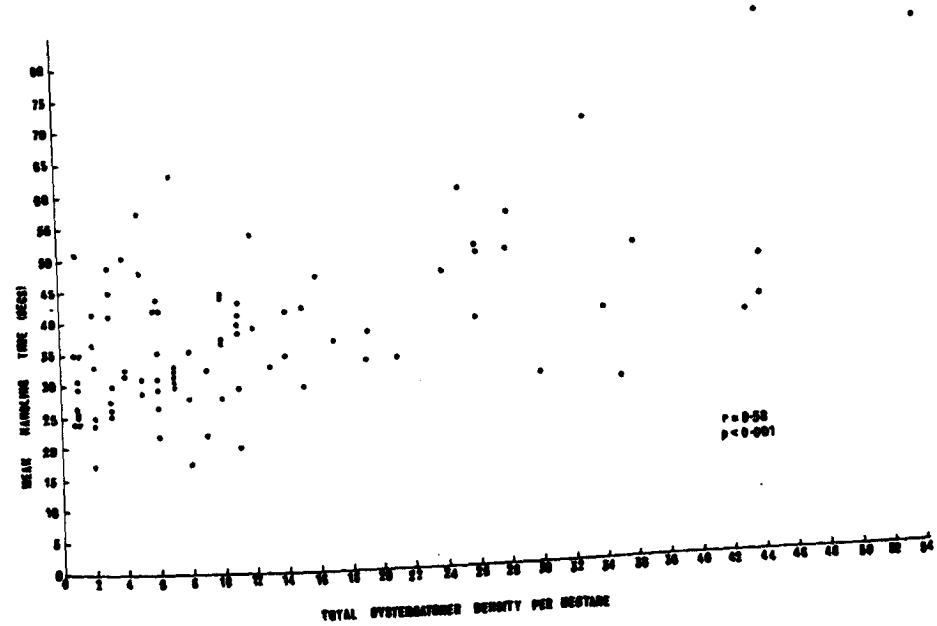


Fig. 6.4 The relationship between mean handling time and oystercatcher density.

Interference between oystercatchers was studied by measuring feeding rate at different oystercatcher densities within one observation site during October-December 1979. The number of cockles taken by a bird in ten minutes and the handling time were measured using the methods described in Chapter 5. A count of the number of birds of each specialisation (using characteristics given in Chapter 5) was made immediately preceeding each estimate of handling time. The methods used for calculating the numerical response and profitability are described in Chapter 8.

(1) Interference

The time taken to handle a cockle increased with oystercatcher density (Fig. 6.4). Birds often picked up their cockle and ran away if another oystercatcher walked nearby - presumably to avoid stealing. This wastes time and is a form of interference but has negligible effect on the feeding rate.

Figures 6.5 and 6.6 show the feeding rate plotted against oystercatcher density. Figure 6.5 uses the number of birds of all specialisations as the independent axis whilst Figure 6.6 uses the number of cockle feeding oystercatchers. In both cases predator density has no effect on feeding rate i.e. there is no interference. The value of the interference constant m is calculated by plotting Log feeding rate against Log number of predators. The slope is equivalent to m. For both sets of results shown the interference constant m = 0.

(2) The ideal free distribution

The model of the aggregative numerical response predicts, when the interference constant m equals nought, that all the predators would feed within the site with the most prey (Fig 6.2). This is clearly not the case, the highest density of birds is at cockle densities of 50-100 cockles per m^2 (Fig 8.4). However, the spatial

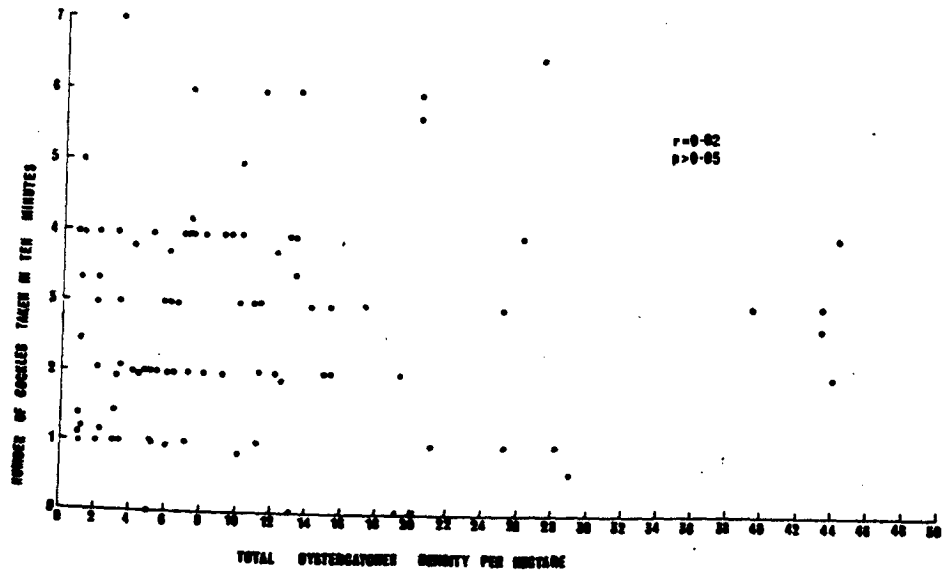


Fig. 6.5 The number of cockles taken per ten minutes in relation to the density of oystercatchers.

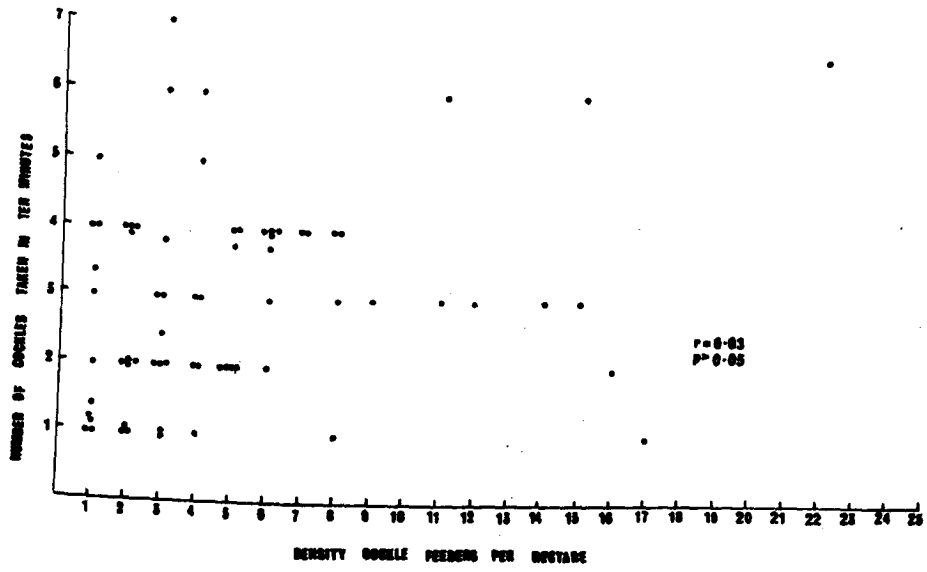


Fig. 6.6 The number of cockles taken per ten minutes in relation to the density of oystercatchers specialising upon cockles.

variations in cockle size and flesh content (see Chapter 1), contradict the assumption of the model that prey composition is equal in all sites. Thus it is not possible to test the model of the aggregative numerical response using this data but it is possible to test the ideal free distribution. As there is no interference the oystercatchers should all feed in the most profitable site if they obey the ideal free distribution. Figure 6.7 shows the oystercatcher density plotted against the profitability of each site. The line shows the distribution predicted by the ideal free distribution. The ideal free distribution does not provide a very close fit of the data: more oystercatchers feed in the poorer areas than would be expected.

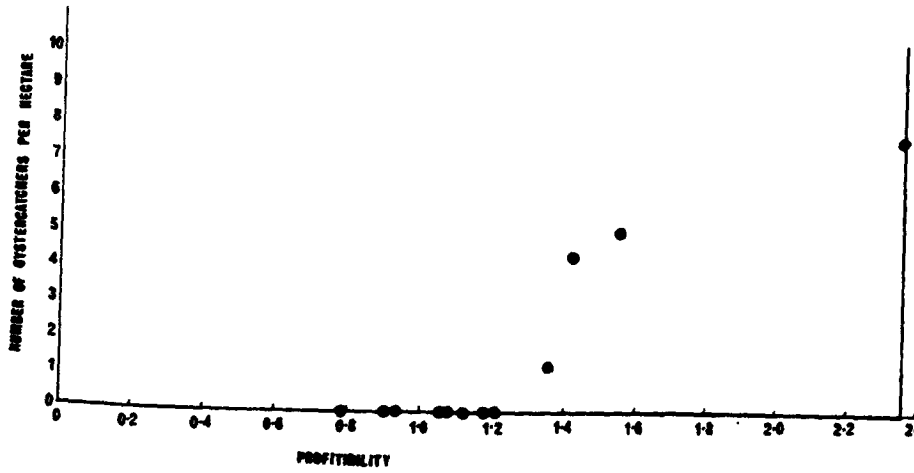


Fig. 6.7 The density of oystercatchers per hectare in relation to the profitibility of each site. The line is the response predicted by the ideal free distribution.

DISCUSSION

The discrepancy between the behaviour predicted by the ideal free distribution and the actual behaviour of the oystercatchers could be due to the birds' need to sample feeding areas repeatedly. The importance of sampling has been stressed by various authors (Krebs et al. 1978; Goss-Custard in press a). This will occur when the prey populations continually change, when the availability changes (e.g. with temperature), or the predator travels widely. The population of cockles is exceedingly constant (Chapter 8), their availability does not appear to fluctuate (Chapter 5) and oystercatchers move little during the winter (Dare 1970). Tinbergen (1976) has shown that starlings Sturnus vulgaris can remember good feeding areas. It thus seems unlikely that oystercatchers should have to spend much time sampling.

Oystercatchers may feed in the less profitable areas because they are excluded by social interactions. Aggressive encounters were recorded in which one bird attacked another nearby. The effect of this on the profitability is difficult to measure especially as it appeared that certain birds were singled out for attack where others were ignored. Such aggression could cause certain birds not to feed in what would otherwise be the most profitable areas. There is evidence that the

proportion of oystercatchers feeding in the poorer areas increases with bird density (Goss-Custard 1977b; Zwarts pers comm) and Vines (1976) has shown that oystercatchers feeding on mussels tend to avoid each other.

SUMMARY

A model is developed which combines the disc equation with the interference equation to describe the aggregative numerical response. It predicts that, if the ideal free distribution is obeyed, then

Number of predators =

constant x number of prey $^{1/\text{degree of interference}}$

This model simplifies the conditions for population stability and predicts the level of spatial density dependence.

Due to correlations between density, size and flesh content within the cockle population at Traeth Melynog, this model could not be directly applied to the data. The major premise of the model was the ideal free distribution and this could be tested. There was no apparent interference between oystercatchers feeding upon cockles so all the oystercatchers should have fed in the most profitable areas. Not all birds did so and it is suggested that they may have been excluded by social interactions.

7. THE NUMERICAL RESPONSE ON THE RIBBLE ESTUARY

INTRODUCTION

The aggregation of waders on the best feeding grounds of an estuary has been widely recorded (Goss-Custard 1970a,1977c; Heppleston 1971; Prater 1972; O'Connor and Brown 1977; Bryant 1979; this study Chapter 6), but the densities of waders in different estuaries may also be related to the distribution of the preferred prey. Goss-Custard *et al.* (1977b) have shown that the densities of redshank and curlew in estuaries in south-east England are correlated with the densities of their main prey species. Wolff (1969) showed that the distribution of many wading birds on the delta of the Rhine and the Meuse (Netherlands) were linked to the distribution of the preferred prey species.

Separating the aggregative numerical response from the population numerical response is a problem that is ignored in most population studies, probably because the contribution of dispersal is often difficult to assess. The differences in populations between estuaries could be attributed to either the aggregative numerical response (waders moving to the estuaries with the most food) or the population numerical response (higher mortality in estuaries with the least food), or a combination of the two. The population of oystercatchers

on the Ribble Estuary was counted each winter between 1970/71 and 1979/80 during which time the cockle population varied dramatically. Unusually, the numbers of birds can be related to changes in the cockle population through time rather than spatially, and this might throw light on whether population or aggregative responses are involved.

METHODS

Preliminary work in the summer of 1976 showed that there were very high densities of cockles on the Southport foreshore but few elsewhere on the Ribble (Lancashire and Western Sea Fisheries report for 1976). Hence the subsequent surveys of the cockle population were restricted to this area (for map see Fig. 7.1). This was also the area in which most of the oystercatchers fed (I.P.Bainbridge in prep).

The cockle population on the Southport foreshore was surveyed by Greenhalgh (1975),and assessed in the Lancashire and Western Sea Fisheries reports for 1977, 1978 and 1979. I surveyed it in the winter of 1979/80 by sampling at ½Km intervals along transects 1Km apart. The samples were washed through a mesh of 7 x 7mm and any cockles retained were counted. Though crude, the inaccuracies in population estimates will be small compared with the enormous change that occured in the cockle population between years.

Greenhalgh's transect through the Southport foreshore produced no cockles and his 154 sampling sites all over the estuary produced an average of only 0.54 cockles (including spat) per m^2. This value is used here as an average density of second winter and older cockles within my study area. This overestimates because many

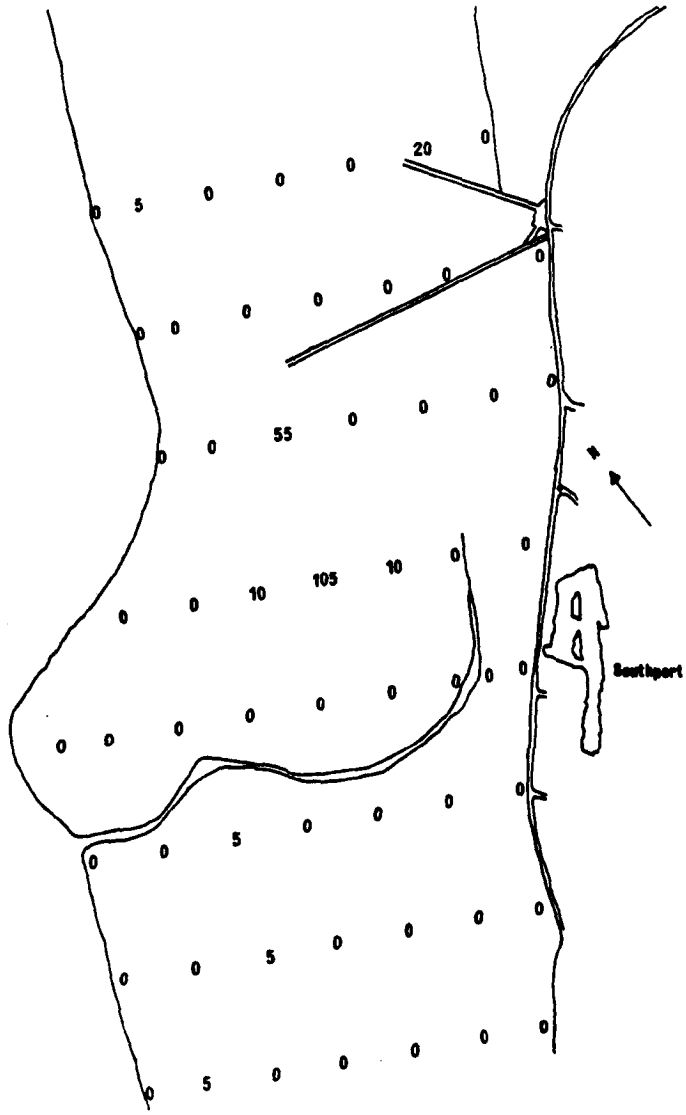


Fig. 7.1 The distribution of cockles (per m^2) at Southport in April 1980. Samples (2 x 1/10 m^2) taken at ½Km intervals along transects 1Km apart.

cockles were undoubtably spat. The estimate of the cockle population on the Southport foreshore as 13.8 million is approximate but as cockles were undoubtably "very sparse" (Greenhalgh 1975), the errors of this survey relative to the estimates for years with abundant cockles are likely to be very small. The cockle population was very low between the 1950's and the spatfall of 1975 (Greenhalgh 1975; Lancashire and Western Sea Fisheries report for 1977; Smith and Greenhalgh 1977) so the estimate of second winter and older cockles derived from Greenhalgh's data was used for the years 1970-1976.

The oystercatcher population has been surveyed since 1970 as part of the Birds of Estuaries Enquiry. Details of the roost sites and census techniques are given in Smith and Greenhalgh (1977).

RESULTS

Figure 7.1 shows the results of my survey in spring 1980. The estimates of the cockle populations for each winter are given in Table 7.1 and Figure 7.2. The cockle population shows a massive increase following the spatfall in 1975 (Lancashire and Western Sea Fisheries report for 1977). This was followed by a massive increase in the oystercatcher population in winter (Fig 7.3) so that the size of the two populations is closely correlated ($p<0.001$, Fig. 7.4).

In 1978 an area of high cockle density was found opposite Lytham St. Annes on the north side of the Ribble. These cockles were almost entirely from the 1975 spatfall and as they were not present in 1976 it was suggested that they had been transported from the Southport foreshore during gales. The live weight present in 1978 was estimated at 5,000 tonnes, compared with 5,800 tonnes present at Southport (Lancashire and Western Sea Fisheries report for 1978). Hence the total population on the Ribble in 1978/79 and 1979/80 was likely to be approximately double that stated in Table 7.1 and the figure stated for 1977/78 is probably also an underestimate. However correcting Figure 7.4 for the Lytham St. Annes population would improve the relationship and increase r^2.

Winter	Number of cockles	Authority	Number of oystercatcher in Dec*
1970/71	13.8×10^6	Greenhalgh (1975)	966
1971/72	13.8×10^6	" "	1533
1972/73	13.8×10^6	" "	2015
1973/74	13.8×10^6	" "	3750
1974/75	13.8×10^6	" "	2624
1975/76	13.8×10^6	" "	5312
1976/77	4804×10^6	LWSF report for 1976	20861
1977/78	1100×10^6	LWSF report for 1977	11507
1978/79	322×10^6	LWSF report for 1978	7105
1979/80	115×10^6	This study	7930

Table 7.1 The number of cockles at Southport and the number of oystercatchers on the Ribble during 1970-1980

* Data provided by Dr. P.H.Smith

Fig. 7.2 The cockle population on the Southport foreshore between 1970/71 and 1979/80.

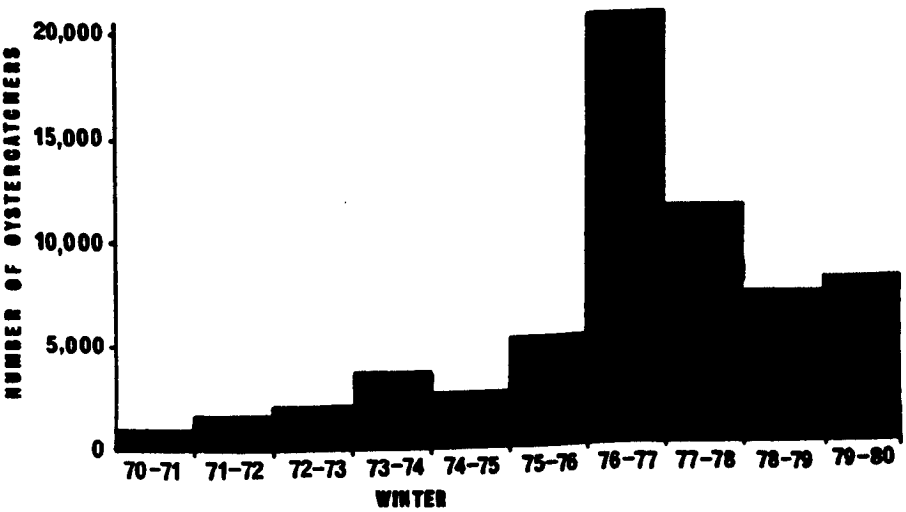


Fig. 7.3 The number of oystercatchers on the Ribble in December of each winter between 1970/71 and 1979/80.

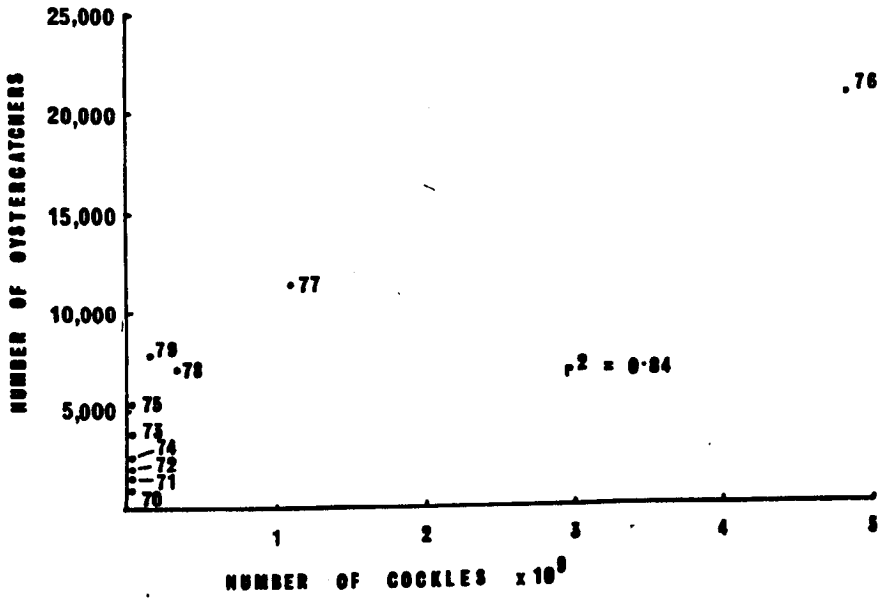


Fig. 7.4 The number of oystercatchers on the Ribble each December in relation to the cockle population at Southport.

Oystercatchers have been caught, aged and ringed at Southport on a number of occasions since 1975 by the South West Lancashire Ringing Group. Table 7.2 shows that there was a high proportion of young birds during the winter of 1976/77 contrasting with a very small proportion two years later when the oystercatcher population was declining. There were no ringing recoveries which would have helped to explain the origin of the extra birds which were present in 1976/77.

Date	Juvenile	Immature	Adult	Means of capture
30/9/75	2		1	mist net
18/11/75			1	mist net
22/9/76	1	1		mist net
20/10/76	1			mist net
24/10/76	33	11	14	cannon net
19/3/77	6	8	19	cannon net
2/12/78		13	177	cannon net
16/12/78			4	mist net
15/4/79			1	mist net

Summary

Winter	Juvenile	Immature	Adult
75-76	2		2
76-77	41	20	33
77-78			
78-79		13	182

Table 7.2 The number of each age class of oystercatcher caught on the Ribble. (Juvenile = hatched within last year. Immature = hatched between 1 and 2 years ago. Adult = hatched more than 2 years ago).

DISCUSSION

Goss-Custard et al.(1977b) proposed four mechanisms by which the number of birds in one estuary could become related to the density of food.

(1) The same group of birds and their descendents return each year to one estuary and no other and their numbers are determined by the food supply there, either directly through starvation or indirectly through affecting subsequent breeding success.

(2) Birds arriving in autumn settle in similar densities in all estuaries but subsequently die of starvation at a disproportionately high rate in estuaries where the preferred food is scarce.

(3) The birds respond behaviourally to the density of the prey in different estuaries and disperse themselves in relation to it during autumn and winter, but their survival is independent of food abundance.

(4) The birds disperse themselves in relation to the density of food in different estuaries but subsequently die disproportionately in estuaries where food is scarce.

Basically, possibilities (1) and (2) are population processes involving survival and reproductive success of birds wintering in each estuary, whereas possibility (3) involves dispersion processes which determine the distribution of birds between estuaries, while (4) is

a combination of both.

The mortality of waders appears to be very low during the winter (Goss-Custard in press b) so that population processes such as (1) or (2) must either take place slowly (for 1) or have very little effect (for 2). So if wader populations respond to rapid changes in food supply, dispersal is probably most important. Since the number of oystercatchers changed so rapidly with prey density on the Ribble, it is likely that dispersal was mainly responsible.

Previous workers have shown that oystercatchers rarely change their feeding grounds. Dare (1970) studied the movements of birds in Wales and North-West Englend whilst Anderson and Minton (1978) analysed the results from ringing on the Wash. Both studies showed that oystercatchers usually returned to the same estuary each winter. The lack of movement recorded in Dare's study was used by the M.A.F.F. to support the suggestion that, if oystercatchers were culled, they would not be replaced by others from elsewhere. This study suggests that in North-West England this site fidelity may not occur in the presence of fluctuations in the food supply. If oystercatchers will move between estuaries to exploit good feeding areas, it is equally likely that they will move to exploit feeding areas from which the competitors

have been removed.

This study contrasts with the study on the Burry Inlet (Horwood and Goss-Custard 1977) where there was no correlation between oystercatcher density and the density of second winter cockles. This discrepancy could be due to the isolation of the Burry Inlet (see Murton 1976): there are no nearby estuaries with comparable numbers of oystercatchers. By contrast, the Ribble has many large flocks nearby (Morecambe Bay, Dee and Lavan Sands, North Wales). Thus if oystercatchers were culled on the Burry Inlet they would probably not be replaced by birds from other estuaries.

Much of the change in the oystercatcher population following the increased cockle population may have been due to an influx of juveniles searching for suitable sites. Pienkowski (1976) suggested that, in Morocco, juvenile dunlin fly between estuaries until they find a suitable one, they then return to this estuary each winter. Baker (1978) proposed that it is a general rule that juvenile animals disperse to discover suitable breeding or wintering grounds which, once found, they return to each year. Catches of oystercatchers on the Ribble indicated that during the massive increase in the oystercatcher population in the winter of 1976/77 there was a very large proportion of juveniles and immatures; two years later,

when the population was in decline there were very few juveniles and immatures - presumably they had found somewhere else. Although it is unlikely that the population increase could be explained entirely in terms of the movement of young birds, it suggests that young birds are most likely to seek the best estuary whilst adults are likely to return to the one they found whilst younger.

A change in diet was associated with the change in cockle stocks on the Ribble. Prior to 1975, the oystercatchers very rarely took cockles but fed mainly on Macoma balthica and Scrobicularia plana (Greenhalgh 1975). Observations in the winter of 1977/78 on the southern side of the estuary showed that the birds were feeding exclusively on cockles. Similar switches in diet from cockles to Macoma and earthworms and then back to cockles were recorded widely following the crash and subsequent recovery of the cockle population after the 1962/63 winter (Hulscher 1964; Dare 1966; Davidson 1967; Dare and Mercer 1973).

SUMMARY

A considerable cockle spatfall in 1975 led to a dramatic, short-lived increase in the cockle population on the Ribble Estuary. There was a parallel fluctuation in the numbers of oystercatchers. The correlation between the two was high.

This study contrasts with that on the Burry Inlet where the numbers of oystercatchers did not vary with the number of cockles. It appears that dispersal is an important factor determining the number of birds on the Ribble, yet other population processes appear to affect the Burry Inlet oystercatchers.

Much of the increase in the oystercatcher numbers was due to the immigration of young oystercatchers. Few young oystercatchers were present when the oystercatcher population was declining.

8. POPULATION DYNAMICS

INTRODUCTION

Current theory suggests that the effect of predators on the population dynamics of prey depends a great deal on the predators behaviour, yet these topics have usually been considered in isolation. So far in this thesis, the behaviour of oystercatchers has been discussed in relation to the variations in prey density and size. This section examines how this behaviour affects the pattern of mortality inflicted on the prey.

Depletion models

Royama (1971b) has attempted to construct a model to predict the general pattern of predation. In his mathmatical model it is assumed that the predators behave ideally and that there is no interference. In other words, he asks what the pattern of prey mortality would be if the predators followed the line for no interference in Figure 6.2 (see Fig. 8.1). Thus the predators feed entirely in the areas with the highest prey density. Assuming there is no replenishment of the prey population during the study period, heavy predation in the areas of high prey density will deplete prey to densities similar to those found in other areas, which will then also be used by the predator. At any point in time, the areas in which the predators feed

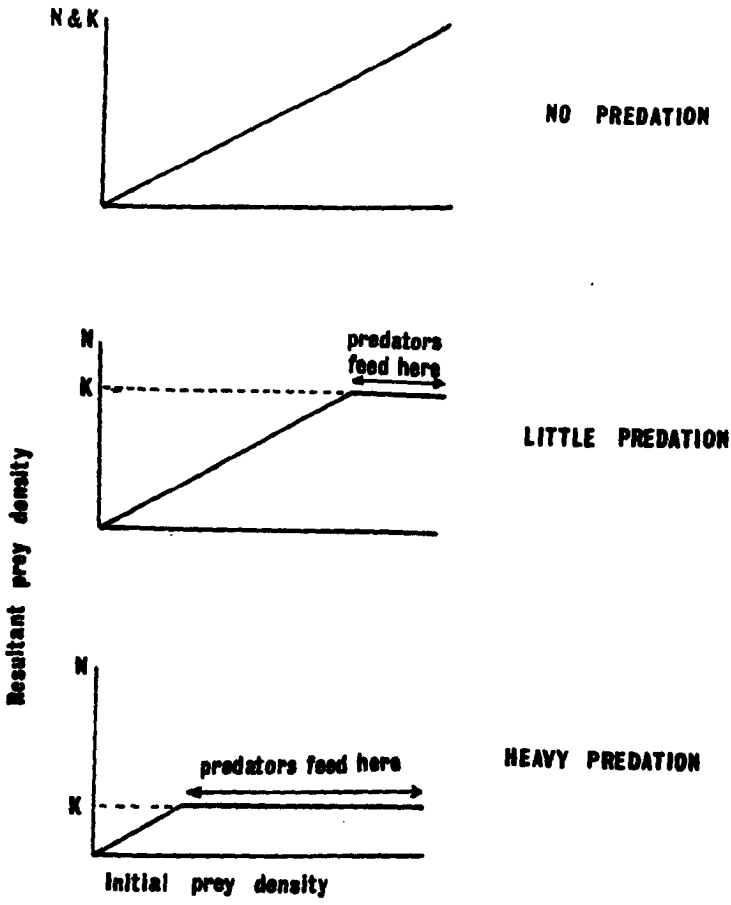


Fig. 8.1 The pattern of predation assumed by Royama's (1971b) model and the depletion model. See text for details. N= initial prey density. K = final prey density.

will have similar prey density and the other areas will be ignored. Plotting final prey density against initial prey density will show a linear rise to a plateau (Fig. 8.1).

The response produced by Royama's model depends largely on the assumption that each prey density is equally frequent. A more realistic model can be made if a measure (f_i) of the frequency of patches of each prey density is included.

The level of the plateau to which the prey are predated can be calculated (Sutherland and Anderson in prep. See appendix II for derivation): the time taken to deplete the maximum prey density M to a level K is

$$t_{M,K} = Th \sum_{j=K+1}^{M} (j-K) f_j + \frac{1}{a'} \sum_{j=K+1}^{M} f_j \log (j/K)$$

Where Th is the handling time and a' is the attack constant.

This model can be used to describe the level to which any prey population will be grazed down by predators behaving optimally. The negative binomial distribution provides a convenient and realistic description of prey distribution (Pielou 1969; Southwood 1976), so the

result of starting with a negative binomial distribution of prey densities is currently being incorporated into the model.

Both Royama's mathmatical model and the model proposed here are only applicable to predators which accumulate in the areas of highest prey density and feed entirely in that area. Such behaviour is most likely to be shown by species which are highly mobile, show no interference and form dense flocks. The behaviour of relatively solitary animals cannot be described by these models, and so the adaptation of Royama's model to describe the predation of shrews and the parasite Ernarmonia conicolana (Royama 1971b) is inappropriate. The application of Royama's model by Goss-Custard (1977c) to redshanks feeding on Corophium volutator is also inappropriate, since Figure 3 of that paper demonstrates how the behaviour of redshanks deviates considerably from the ideal manner assumed in Royama's model.

Those predator-prey models which describe spatial variation in prey mortality e.g. Royama (1971b); Chapter 6; section above; assume that each predator can always feed where it chooses and the size and energy content of the prey do not vary with density. Both of these assumptions do not hold for the oystercatchers feeding upon cockles at Traeth Melynog. The first

because areas of shore are exposed for different periods due to tidal flow, and the second because the profitability of the different areas is not related to cockle density in a simple fashion. What effect does this have on the pattern of mortality of the prey?

In order to estimate the effect of predation of cockles by oystercatchers at each site, it was necessary to measure:

(1) The feeding rate at each site (the functional response).

(2) The number of bird/minutes spent by oystercatchers foraging for cockles at each site during each daylight tide (the numerical response).

(3) The distribution of birds and the feeding rate at night.

(4) Seasonal changes in the number of oystercatchers specialising on cockles present at Traeth Melynog.

(5) The cockle density at each site at the beginning and end of the study period (beginning of December 1978 to the beginning of April 1979).

The functional response

The feeding rate was measured at each site. The methods are described in Chapter 5.

The aggregative numerical response

This was assessed in two ways. Firstly, the cockle specialists were counted in each site once all the sites had been uncovered by the tide. This showed the bird distribution when they had the option of feeding in any site. Secondly, the number of

oystercatchers feeding on cockles within a site was counted at approximately twelve minute intervals (between the estimates of feeding rates - see Chapter 5) during all the time that birds spent in that site (usually dictated by the covering or uncovering of the tide and the movement of birds up or down the shore). The number of bird/minutes spent in that site was calculated by multiplying the mean oystercatcher density in that site by the length of time birds were present there.

The feeding behaviour at night

Measurements of feeding rate were made using an image intensifier telescope at observation site B (Fig 1.1), mainly in the winter of 1979-80. Stalking birds proved impossible and the only method that yielded any data was to sit on the upper edge of an observation site about two hours before the tide covered it and wait for the birds to be forced towards me. The birds had to be within about fifty metres before I could confidently count the number of cockles taken and about ten minutes later, when they were within about twenty five metres of me, they flew off.

I also counted the numbers feeding at night, but it was difficult to identify cockle specialists during the night, so the totals refer to all birds feeding, and therefore all specialisations. Counts were made during the day for comparison.

Seasonal changes in the number of oystercatchers specialising upon cockles.

The seasonal change in the number of oystercatchers feeding on cockles was estimated throughout the winter of 1978/79 by counting the number of cockle feeding birds during the ebb or flood tide, when practically all the birds were feeding (see Fig. 8.6). The number of birds not feeding was also counted. The number of resting cockle feeders was estimated as:

Number of cockle feeders not feeding =

$$\text{no birds not feeding} \times \frac{\text{no cockle specialists feeding}}{\text{no birds feeding}}$$

This assumed that there were the same proportion of cockle feeders amongst the birds resting as amongst those feeding. However, as practically all the birds were feeding it would make little difference if this assumption proved false.

Cockle density at the beginning and end of the winter

The cockles in each site were sampled at the end of November/beginning of December 1978 and the end of March/beginning of April 1979. The methods are described in Chapter 3. The difference between the two sets of samples gives an estimate of the mortality during this period.

(a) The functional response

The functional response was type II: the number of cockles taken in ten minutes increases rapidly with an increase in cockle density up to a density of approximately ninety cockles per square metre; after this, the number taken increases only slowly (see Chapter 5 for full details).

(b) The aggregative numerical response

The distribution of predators is likely to depend upon spatial variations in the prey population. As Chapter 3 describes, it is not just cockle density which varies, there are also trends down the shore in cockle size and ash free dry weight (AFDW). In order to understand the numerical response, it is necessary to know how the profitability (expressed as biomass intake) varies with density. The profitability for each site can be calculated as

Profitability =

feeding rate x ($\%_{\text{of diet}}$ x AFDW) of each size class

The change in the feeding rate with cockle density is described by the functional response (see above). How does size taken and AFDW vary with density?

Chapter 4 showed that large cockles were preferred, but some smaller ones were also taken at a

rate depending partly upon their own density. Thus at high cockle densities (where more small cockles are present - see Chapter 3), the mean size taken is smaller (Fig. 8.2). This decrease in cockle size may appear insignificant, but as the AFDW increases exponentially with shell length (Fig. 4.2) a small decline in the mean size may have a considerable effect on the amount of flesh eaten. As larger cockles are taken at low prey densities, the areas of high cockle densities need not necessarily be the most profitable.

The AFDW for a given sized cockle increases down the beach, while cockle density decreases down the beach (Chapter 3). Thus AFDW is negatively correlated with cockle density (Fig. 3.7). A cockle from an area of high density will be far less profitable than the same sized one from an area of low cockle density.

Figure 8.3 shows the relationship between profitability (calculated from the above equation) and cockle density. At high cockle densities many cockles are taken but they are small and contain little flesh. At very low cockle densities the predated cockles are large and contain a lot of flesh (relative to their size) but only a few are taken per ten minutes. Profitability is at its maximum level at a medium density of 25-100 cockles per m^2.

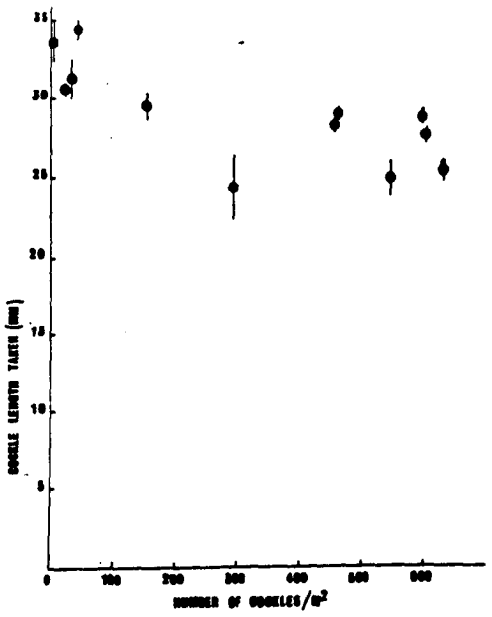


Fig. 8.2 The relationship between mean cockle size taken and cockle density. Each point refers to one site.

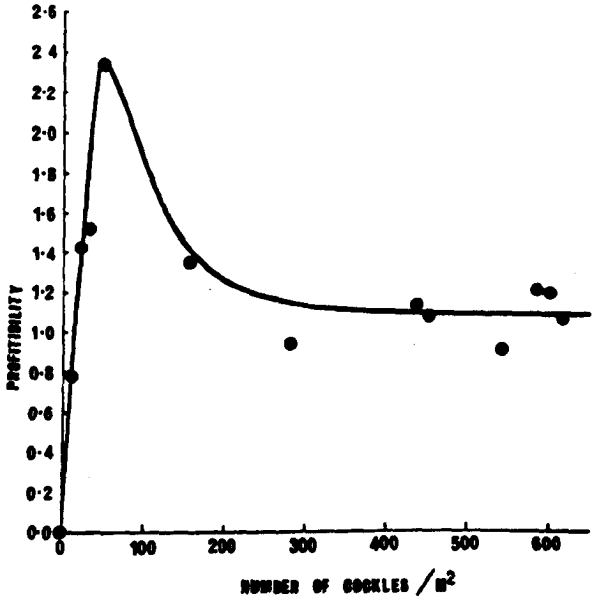


Fig. 8.3 The profitability (grams ash free dry weight eaten per ten minutes) in relation to cockle density.

The aggregative numerical response (Fig. 8.4) corresponds with the variation in profitability. The peak oystercatcher density is at about 50 cockles per m^2. This contradicts the theoretical response which is a maximum predator density at the highest prey density (Royama 1971b; Hassell and May 1973; Chapter 6). Although the oystercatchers are not selecting the sites with the highest prey density, they are selecting the most profitable ones (Fig. 8.5). This relationship is statistically significant ($p<0.01$ Spearman rank correlation coefficient).

Oystercatchers at Traeth Melynog feed near the water's edge. Is this because feeding rate is better there or are they just trying to feed as low down the shore as they can? Feeding is only marginally better (if at all) near the water's edge than on the same area after a period of exposure (Fig. 5.1). The regression line suggests that a site at the top of the shore is 9% less profitable when the tide is at the sites 250m lower down than when the tide is nearby. The difference in profitability down the shore greatly exceeds any difference in feeding rate due to higher sites being exposed for longer: oystercatchers seem to prefer feeding lower down because feeding is better there. It seems likely that oystercatchers at Traeth Melynog follow the tide simply because it is the lowest down the shore they can be.

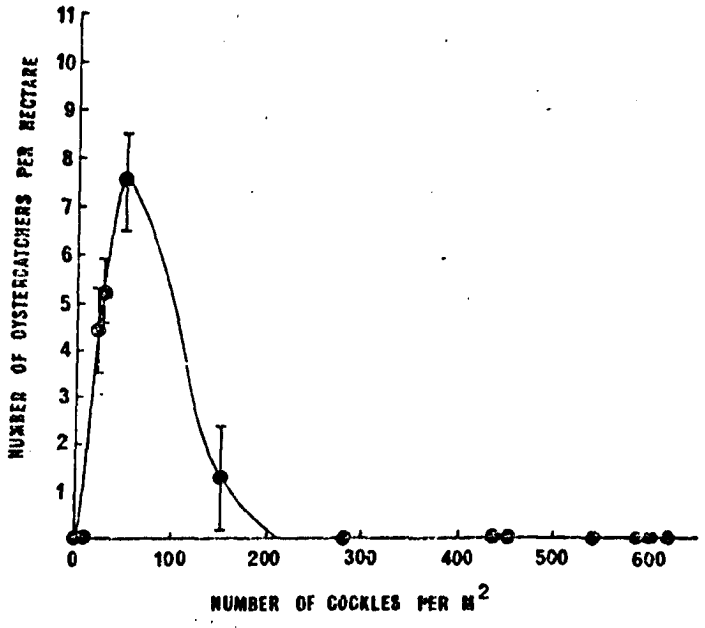


Fig. 8.4 The number of cockle feeding oystercatchers per hectare in relation to the cockle density.

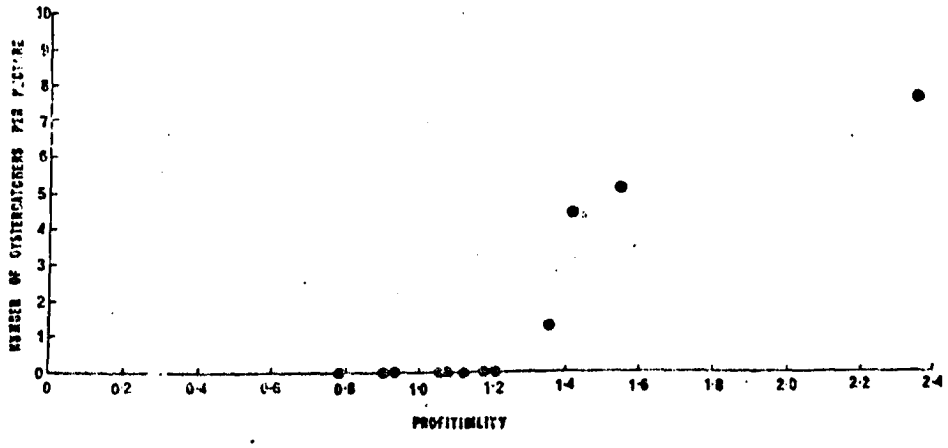


Fig. 8.5 The density of cockle feeding oystercatchers in relation to the profitability (grams ash free dry weight eaten per ten minutes) of each site.

Counts made every twenty five minutes showed that there was a bimodal pattern in the number of oystercatchers feeding upon cockles (Fig. 8.6). They fed during the ebbing and flood tide but fed little at high and low tide. This can be interpreted in terms of hunger: when the tide ebbs, the birds have not fed for five hours so they feed in the first areas exposed even if these are not the most profitable. As the tide floods, they feed knowing they cannot feed for another five hours.

The aggregative numerical response shown in Figure 8.4 describes the distribution of birds at low tide but in order to understand the pattern of cockle mortality we must include the time oystercatchers spend feeding whilst the preferred sites are covered by the tide. Figure 8.7 shows the number of bird/minutes spent in each site during each tide. This shows that the total time spent by feeding oystercatchers is greatest in the areas of fairly low cockle density.

(c) Night feeding

Table 8.1 shows the number of birds feeding in site B during the day and night. As many birds were feeding at night as were feeding during the day. During the night it was difficult to classify the birds according to their prey specialisation but since

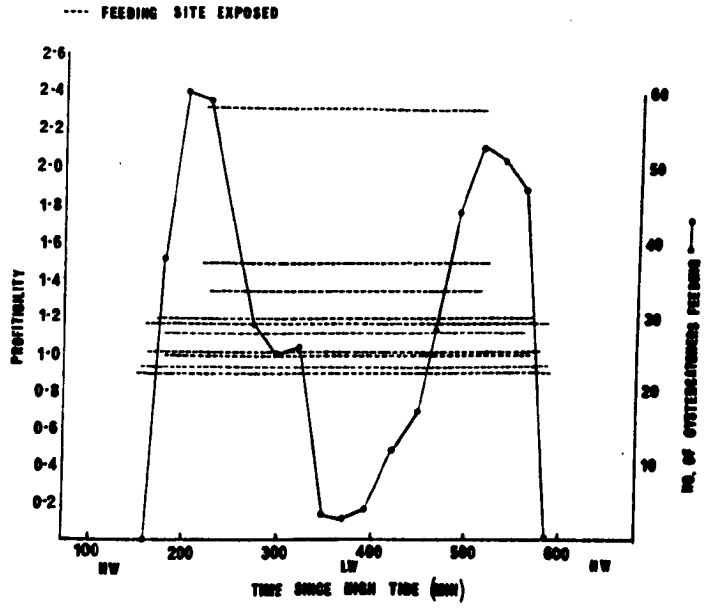


Fig. 8.6 Number of oystercatchers feeding at twenty five minute intervals through the tidal cycle. The length of time feeding sites were exposed is shown in relation to their profitability.

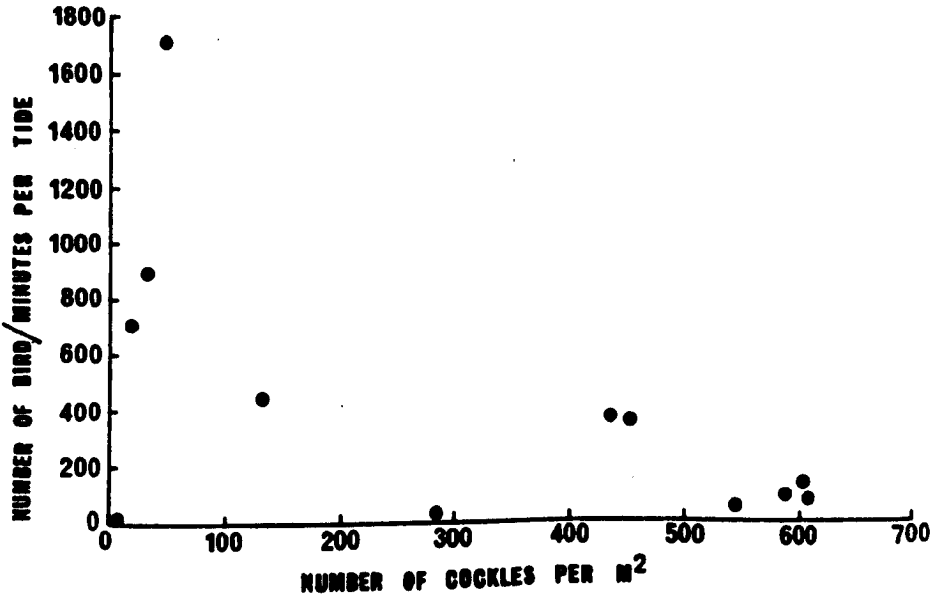


Fig. 8.7 The total time spent by oystercatchers feeding upon cockles in each observation site each daylight tide in relation to cockle density.

	DAY	NIGHT
Maximum no of birds feeding	6.2 ± 1.3	3.2 (18 in 55 mins)
Feeding rate	20.0 ± 2.3	22.2 ± 4.8

Table 8.1. A comparison of day and night feeding.

practically all the birds were feeding, it is likely that as many birds were feeding on cockles during the night as during the day.

Table 8.1 also shows the comparative feeding rate during night and day. Oystercatchers feed at about half the rate during the night that they do during the day.

(d) Seasonal changes in the numbers of oystercatchers

Figure 8.8 shows the number of cockle feeding oystercatchers at Traeth Melynog during 1978/79. The cockle feeding birds did not arrive until late September/early October and left in March April. Most of the summering population consisted of juveniles or immatures and these fed on S.plana and worms.

(e) Predicted pattern of loss

The pattern of cockle predation can be determined by combining the functional response with the amount of time oystercatchers spend feeding at each site. Figure 8.9 shows the proportion of cockles removed during each

daylight tide.

The data on the aggregative numerical response was collected in January and February. There were more oystercatchers present in December but fewer in March (Fig. 8.8). These differences balance each other out so the results for January-February can be used for the entire period 1st December - 31st March. Thus the number of cockles taken per tide can be multiplied by 240 (two tides a day) to give the predation over the entire period.

This calculation must be modified to include the lower predation rate at night. Oystercatchers at Traeth Melynog spend as much time feeding at night as they do during the day. During November to March there is a mean of ten hours daylight a day hence there will be 140 tides in darkness and 100 tides in daylight. Oystercatchers feed at half the rate during the night so predation during night tides during this period is equivalent to 140/2 = 70 daylight tides. Thus predation during this period is equivalent to 100 + 70 = 170 daylight tides.

Figure 8.9 shows the pattern of cockle mortality inflicted by the oystercatchers. The percentage taken varied between 28% at 45 cockles per m^2 and almost 0% at 12 and 600 cockles per m^2. Thus over most of the

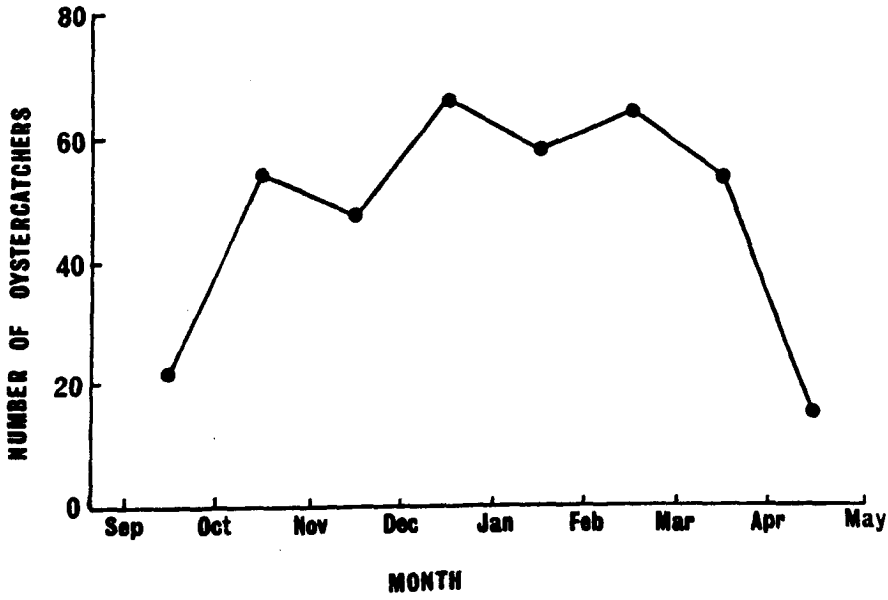


Fig. 8.8 Seasonal changes in the number of cockle feeding oystercatchers in the winter of 1978-79.

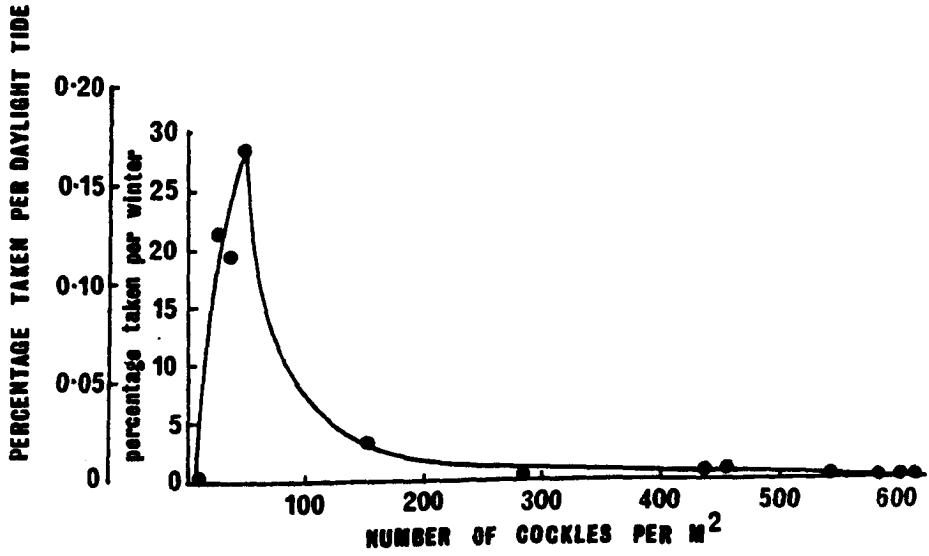


Fig. 8.9 The calculated percentage predation of cockles per tide and per winter in relation to cockle density.

range of cockle densities (45 - 600 cockles per m^2) the mortality was inversely density dependent.

(f) Actual change in cockle density over the winter

The percentage loss of cockles from each site is plotted against the density at the start of the winter in Figure 8.10. The loss of cockles from each site is small but the predicted pattern of mortality was not shown. The downshore movement of cockles described in Chapter 3 would counter the effects of predation at the bottom of the shore.

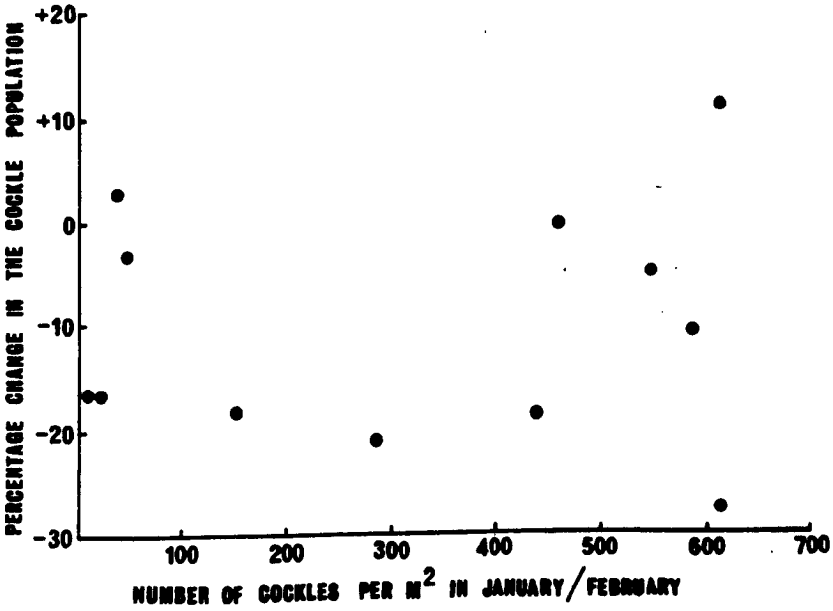


Fig. 8.10 Percentage change in the cockle population in relation to the cockle population in January/February

DISCUSSION

The few previous studies that have combined studying the predator's behaviour and estimating prey mortality have usually shown that the predator inflicts spatial density dependent mortality. Goss-Custard (1977c) found that redshanks feeding on Corophium volutator showed a type II functional response but collected in the areas of highest prey density and so inflicted a density dependent mortality. The recorded pattern of mortality was consistent with this. Similarly East and Pottinger (1975) showed that starlings spent far more time in the areas of high densities of the grass grub Coslelytra zealandica and so inflicted density dependent mortality. In accordance with this, the number of prey disappearing over the winter was also density dependent. Hassell (1980) studied the parasitism of the winter moth Operophtera brumata by Cyzenis albicans and also found that the parasite inflicted spatially density dependent mortality by spending a disproportionate amount of time at higher prey densities.

The mortality was low compared with the high cockle mortality on the Burry Inlet (Hancock and Urquhart 1965) and on Strangford Lough (O'Connor and Brown 1977). The difference will be due to the lack of cockle fishing at Traeth Melynog and to the relatively

small number of oystercatchers present. The factors affecting the total numbers present at Traeth Melynog were not investigated.

Cole (1956) noted that cockles over four winters old are very scarce in heavily exploited populations but that ones twice this age are regularly encountered in unexploited populations. The large number of old cockles found at Traeth Melynog (Fig. 3.1) is in accordance with this for there was negligible mortality caused by fishing and although oystercatchers took old cockles they only removed a small proportion of them.

The models described in this thesis, in common with practically all other foraging models, have assumed that prey size and flesh content did not vary with density. At Traeth Melynog these assumptions were incorrect so the models could not be applied. In other studies on mudflats, prey size was correlated with density (Goss-Custard 1969, 1977a,b). The distribution of plant weights is affected by density in a predictable manner (Harper 1977) which may be applicable to all sessile prey. Thus the assumption that prey size is independent of density may only rarely be true outside laboratory experiments. It seems likely that future models must not depend upon this assumption if they are to be of general use in predicting the behaviour of predators in the field.

SUMMARY

An algebraic model is developed which describes prey depletion for a predator showing no interference and behaving ideally.

At night oystercatchers fed as actively as they did during the day but extracted cockles at half the rate.

The profitability (defined as biomass intake) of each site depended not only on cockle density but also on cockle size and flesh content. At high cockle densities many cockles are taken but they are small and contain little flesh (relative to their size). At very low cockle densities the predated shells are large and contain a lot of flesh but only a few are taken per ten minutes. At a medium density of 25-100 cockles per m^2 the profitability is at its maximum level.

Oystercatchers fed most in the areas of highest profitability (i.e. 25-100 cockles per m^2 and so inflicted the highest mortality in these areas. The proportion of the cockles predated between 1st December and 31st March was estimated as between 28% (at 45 cockles per m^2) and virtually 0% (at 12 and 600 cockles per m^2).

The actual disappearance of cockles did not show any relationship with density. The downshore movement of cockles would counter the effects of predation in the most profitable sites at the bottom of the shore.

The large number of old cockles at Traeth Melynog is in accordance with the low mortality caused by the oystercatchers and the absence of cockle fishing.

In the field prey size and flesh content may often vary with density, as in this study, yet practically all foraging models assume they do not. I suggest future models should not assume prey size is independent of density if they are to be of general use in predicting the behaviour of predators in the field.

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APPENDIX I

Derivation of aggregative numerical response model

$$a = Q\, b_i^{-m}$$

and

$$a = a' Ts$$

therefore

$$a' = \frac{Q\, b_i^{-m}}{Ts}$$

this can be substituted into the disc equation

$$Na = \frac{a'\, \alpha_i\, T}{1 + a'\, \alpha_i\, Th}$$

so that

$$Na = \frac{Q\, b_i^{-m}/Ts\ \alpha_i\, T}{1 + Q\, b_i^{-m}/Ts\ \alpha_i\, Th}$$

$$Na + \frac{Q\, b_i^{-m}}{Ts}\, \alpha_i\, Th\, Na = \frac{Q\, b_i^{-m}}{Ts}\, \alpha_i\, T$$

$$\frac{Na\, Ts}{Q\, b_i^{-m} \alpha_i} + Th\, Na = T$$

$$\frac{Ts}{Q\, b_i^{-m} \alpha_i} + Th = \frac{T}{Na}$$

$$\frac{Ts}{Q\, b_i^{-m} \alpha_i} = \frac{T}{Na} - Th$$

$$\frac{Ts}{Q\, b_i^{-m} \alpha_i} = \frac{T - Th\, Na}{Na}$$

$$\frac{Q\, b_i^{-m} \alpha_i}{Ts} = \frac{Na}{T - Th\, Na}$$

$$\frac{Q\ b_i^{-m}\ \alpha_i}{Ts} = \frac{Na/T}{1 - (Na/T)\ Th}$$

$$Q\ b_i^{-m} = \left(\frac{Na/T}{1 - (Na/T)\ Th}\right)\frac{Ts}{\alpha_i}$$

Q and Th are constants. Na/T and Ts are constants if the ideal free distribution is obeyed. Thus

$$b_i^{-m}\ \alpha\ \frac{1}{\alpha_i}$$

$$b_i = k\ \alpha_i^{1/m}$$

APPENDIX II

Prey depletion model (W.J.Sutherland and C.W.Anderson)

Prey density varies between areas and has possible values 1,2,.....M. f_i is the total area in which prey density is i. Thus $\sum_{i=1}^{M} f_i$ = total area of the whole region.

The rate at which depletion takes place will be progressively slowed by two factors. Firstly, predation extends over a larger area (Fig. 8.1). Secondly, at lower prey densities the feeding rate will be reduced.

The number of prey taken (Na) in time T at prey density α is given by the disc equation (Holling 1959b)

$$\frac{Na}{T} = \frac{a' \alpha}{1 + a' \alpha Th}$$

where Th is the handling time and a' the attack constant. Thus

$$\frac{Na}{T} = \frac{\alpha}{\alpha Th + 1/a'}$$

The rate at which prey density is reduced over an area A is

$$\frac{Na/T}{A} = \frac{\alpha}{A(\alpha Th + 1/a')}$$

Let $\alpha(t)$ denote the maximum prey density at time t after feeding starts. Then $\alpha(0) = M$ and initially the rate of change of $\alpha(t)$ is

$$\frac{d\alpha(t)}{dt} = \frac{-\alpha(t)}{f_M\,(\alpha(t)\,Th + 1/a')}$$

The minus sign appears because $\alpha(t)$ is decreasing. This equation will hold true until the prey density over the area f_M has been reduced to M-1 i.e. so long as $M \geqslant \alpha(t) \geqslant M-1$. After this, feeding will extend over an area $f_M + f_{M-1}$, and so

$$\frac{d\alpha(t)}{dt} = \frac{-\alpha(t)}{(f_M + f_{M-1})(\alpha(t)\,Th + 1/a')}$$

for $M - 1 \geqslant \alpha(t) > M - 2$

In general

$$\frac{d\alpha(t)}{dt} = \frac{-\alpha(t)}{(f_M + \ldots\ldots + f_{M-r})(\alpha(t)\,Th + 1/a')} \qquad (1)$$

for $M-r \geqslant \alpha(t) > M-r-1$. $r=0,1,\ldots\ldots M-1$.

Rearrangement of (1) gives

$$(f_M + \ldots\ldots f_{M-r})\left(Th + \frac{1}{a'\,\alpha(t)}\right)\frac{d\alpha(t)}{dt} = -1 \qquad (2)$$

for $M-r \geqslant \alpha(t) > M-r-1$. $r = 0,1,\ldots\ldots M-1$.

Let t_M, t_{M-r} denote the time for maximum prey density to reduce from M to M-r. Intergrating (2) with respect to t between $t_{M,M-r}$ and $t_{M,M-r-1}$, obtains

$$(f_M + \ldots + f_{M-r}) \int_{t_{M,M-r}}^{t_{M,M-r-1}} \left(Th + \frac{1}{a'\alpha(t)}\right)\frac{d\alpha(t)}{dt}\,dt = -\int_{t_{M,M-r}}^{t_{M,M-r-1}} dt$$

That is

$$\left(\sum_{j=M-r}^{M} f_j\right) \int_{M-r}^{M-r-1} \left(Th + \frac{1}{a'\alpha}\right) d\alpha = t_{M,M-r} - t_{M,M-r-1}$$

The difference on the right is the time to reduce maximum prey density from M-r to M-r-1, say $t_{M-r,M-r-1}$. Straightforward intergration gives.

$$t_{M-r,M-r-1} = \left(\sum_{j=M-r}^{M} f_j\right)\left(Th + \frac{1}{a'} \log_e\left(\frac{M-r}{M-r-1}\right)\right)$$

and so

$$t_{M,K} = \sum_{r=0}^{M-K-1} t_{M-r,M-r-1}$$

$$= Th \sum_{r=0}^{M-K-1} \sum_{j=M-r}^{M} f_j + \frac{1}{a'} \sum_{r=0}^{M-K-1} \sum_{j=M-r}^{M} f_j \log\left(\frac{M-r}{M-r-1}\right) \quad (3)$$

The sums in (3) simplify slightly:

$$\sum_{r=0}^{M-K-1} \sum_{j=M-r}^{M} = \sum_{r=0}^{M-K-1} \sum_{j=0}^{r} f_{M-j'}$$

$$= \sum_{j'=0}^{M-K-1} \sum_{r=j'}^{M-K-1} f_{M-j'}$$

$$= \sum_{j'=0}^{M-K-1} (M-K-j') f_{M-j'}$$

$$= \sum_{j=K+1}^{M} (j-K) f_j$$

and

$$\sum_{r=0}^{M-K-1} \sum_{j=M-r}^{M} f_j \log\left(\frac{M-r}{M-r-1}\right) = \sum_{r=0}^{M-K-1} \sum_{j'=0}^{r} f_{m-j'} \log\left(\frac{M-r}{M-r-1}\right)$$

$$= \sum_{j'=0}^{M-K-1} f_{M-j'} \sum_{r=j'}^{M-K-1} \log\left(\frac{M-r}{M-r-1}\right)$$

$$= \sum_{j'=0}^{M-K-1} f_{M-j'} \log\left(\frac{M-j'}{K}\right)$$

$$= \sum_{j=K+1}^{M} f_j \log\left(\frac{j}{K}\right)$$

Thus (3) becomes

$$t_{M,K} = Th \sum_{j=K+1}^{M} (j-K) f_j + \frac{1}{a'} \sum_{j=K+1}^{M} f_j \log (j/K) \quad (4)$$

The sum $\sum_{j=K+1}^{M} (j-K) f_j$ is the total number of prey taken up to the instant when maximum prey density reaches K. Hence in (4) the first term on the right is just the total handling time of prey taken up to this instant. The influence of searching for prey therefore acts through the second term.

MATHMATICAL SYMBOLS

λ = Encounter rate

E = Energy content

Th = Handling time

θ = Proportion misidentified

Na = Number of prey eaten

a' = Instantaneous search rate

T = Total time

α_i = Number of prey in patch i

b_i = Number of predators in patch i

a = Searching efficiency

Q = Quest constant

m = Interference constant

Ts = Time spent searching

μ = Aggregative constant

Ns = Surviving prey after parasitism

Nt = Total number of prey

Pt = Total number of predators

M = Highest prey density before predation

K = The level to which M is depleted by predation

t = Time predators spend depleting prey

f_i = Frequency of prey density i